Invertebrate Responses to Large-Scale Change: Impacts of Eutrophication and Cataclysmic Earthquake Events in a Southern New Zealand Estuary

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Abstract

Environmental stress and disturbance can affect the structure and functioning of marine ecosystems by altering their physical, chemical and biological features. In estuaries, benthic invertebrate communities play important roles in structuring sediments, influencing primary production and biogeochemical flux, and occupying key food web positions. Stress and disturbance can reduce species diversity, richness and abundance, with ecological theory predicting that biodiversity will be at its lowest soon after a disturbance with assemblages dominated by opportunistic species. The Avon-Heathcote Estuary in Christchurch New Zealand has provided a novel opportunity to examine the effects of stress, in the form of eutrophication, and disturbance, in the form of cataclysmic earthquake events, on the structure and functioning of an estuarine ecosystem. For more than 50 years, large quantities (up to 500,000m^3/day) of treated wastewater were released into this estuary but in March 2010 this was diverted to an ocean outfall, thereby reducing the nutrient loading by around 90% to the estuary. This study was therefore initially focussed on the reversal of eutrophication and consequent effects on food web structure in the estuary as it responded to lower nutrients. In 2011, however, Christchurch was struck with a series of large earthquakes that greatly changed the estuary. Massive amounts of liquefied sediments, covering up to 65% of the estuary floor, were forced up from deep below the estuary, the estuary was tilted by up to a 50cm rise on one side and a corresponding drop on the other, and large quantities of raw sewage from broken wastewater infrastructure entered the estuary for up to nine months. This study was therefore a test of the potentially synergistic effects of nutrient reduction and earthquake disturbance on invertebrate communities, associated habitats and food web dynamics.

Because there was considerable site-to-site heterogeneity in the estuary, the sites in this study were selected to represent a eutrophication gradient from relatively “clean” (where the influence of tidal flows was high) to highly impacted (near the historical discharge site). The study was structured around these sites, with components before the wastewater diversion, after the diversion but before the earthquakes, and after the earthquakes. The eutrophication gradient was reflected in the composition and isotopic chemistry of primary producer and invertebrate communities and the characteristics of sediments across the sample sites. Sites

closest to the former wastewater discharge pipe were the most eutrophic and had cohesive organic-rich, fine sediments and relatively depauperate communities dominated by the opportunistic taxa Capitellidae. The less-impacted sites had coarser, sandier sediments with fewer pollutants and far less organic matter than at the eutrophic sites, relatively high diversity and lower abundances of micro- and macro-algae. Sewage-derived nitrogen had became incorporated into the estuarine food web at the eutrophic sites, starting at the base of the food chain with benthic microalgae (BMA), which were found to use mostly sediment-derived nitrogen. Stable isotopic analysis showed that $\delta^{13}C$ and $\delta^{15}N$ values of most food sources and consumers varied spatially, temporally and in relation to the diversion of wastewater, whereas the earthquakes did not appear to affect the overall estuarine food web structure. This was seen particularly at the most eutrophic site, where isotopic signatures became more similar to the cleaner sites over two-and-a-half years after the diversion. New sediments (liquefaction) produced by the earthquakes were found to be coarser, have lower concentrations of heavy metals and less organic matter than old (existing) sediments. They also had fewer macroinvertebrate inhabitants initially after the earthquakes but most areas recovered to pre-earthquake abundance and diversity within two years. Field experiments showed that there were higher amounts of primary production and lower amounts of nutrient efflux from new sediments at the eutrophic sites after the earthquakes. Primary production was highest in new sediments due to the increased photosynthetic efficiency of BMA resulting from the increased permeability of new sediments allowing increased light penetration, enhanced vertical migration of BMA and the enhanced transport of oxygen and nutrients. The reduced efflux of NH_4-N in new sediments indicated that the capping of a large portion of eutrophic old sediments with new sediments had reduced the release of legacy nutrients (originating from the historical discharge) from the sediments to the overlying water. Laboratory experiments using an array of species and old and new sediments showed that invertebrates altered levels of primary production and nutrient flux but effects varied among species. The mud snail *Amphibola crenata* and mud crab *Austrohelice crassa* were found to reduce primary production and BMA biomass through the consumption of BMA (both species) and its burial from bioturbation and the construction of burrows (*Austrohelice*). In contrast, the cockle *Austrovenus stutchburyi* did not significantly affect primary production and BMA biomass. These results show that changes in the structure of

invertebrate communities resulting from disturbances can also have consequences for the functioning of the system.

The major conclusions of this study were that the wastewater diversion had a major effect on food web dynamics and that the large quantities of clean and unpolluted new sediments introduced to the estuary during the earthquakes altered the recovery trajectory of the estuary, accelerating it at least throughout the duration of this study. This was largely through the ‘capping’ effect of the new liquefied, coarser-grained sediments as they dissipated across the estuary and covered much of the old organic-rich eutrophic sediments. For all aspects of this study, the largest changes occurred at the most eutrophic sites; however, the surrounding habitats were important as they provided the context for recovery of the estuary, particularly because of the very strong influence of sediments, their biogeochemistry, microalgal and macroalgal dynamics. There have been few studies documenting system level responses to eutrophication amelioration and to the best on my knowledge there are no other published studies examining the impacts of large earthquakes on benthic communities in an estuarine ecosystem. This research gives valuable insight and advancements in the scientific understanding of the effects that eutrophication recovery and large-scale disturbances can have on the ecology of a soft-sediment ecosystem.

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Preface

“We sit in the mud... and reach for the stars”

– Ivan Turgenev

Chapter 1

General Introduction

1.1. Large-scale change in the marine environment

The marine environment is a vast and complex system composed of numerous interlinked physical, chemical and biological components. Optimal functioning of the marine realm relies on often intricate and subtle balances and interplays of these various components over wide spatial and temporal scales. Although marine ecosystems are dynamic and are constantly changing, much of this is due to natural variability and fluctuations, and so large-scale changes generally occur only over long time periods (Southward 1995). However, stress and disturbance can cause large-scale change in marine ecosystems over much shorter time scales. These can result from natural perturbations or anthropogenic influences. With the exception of disease outbreak, natural perturbations that cause abrupt change are usually in the form of physical disturbances such as earthquakes, tsunamis, droughts, fires, storms, hurricanes, tornadoes, cyclones, floods, landslides and volcanic eruptions. Although not all instances of these events will cause significant change to marine ecosystems (and many that do are unknown or not reported) there is an increasing literature describing the effects of these often unpredictable events on various facets of the marine environment. For example, studies have reported the effects of hurricanes (e.g., Vanselow et al. 2007, Alvarez-Filip et al. 2009, Engle et al. 2009, Scheibling et al. 2010) and tsunamis (Szczucinski et al. 2006, Bahlburg and Weiss 2007, Prathep et al. 2008, Whanpetch et al. 2010, Tanabe and Subramanian 2011, Miura et al. 2012, Sathianandan et al. 2012, Takami et al. 2013) on various physical, biological and ecological aspects of the marine environment.

Many of the changes that occur in marine environments are, however, driven by anthropogenic influences rather than by natural perturbations. A large literature reports the effects of climate change, fisheries exploitation, oil spills, pollution, sedimentation, El Niño-Southern Oscillation (ENSO), habitat loss/alteration, coastal infrastructure and invasive species on marine ecosystems. With the exception of oil spills, anthropogenically induced changes to marine ecosystems are usually not immediate (i.e., occur on the time-scale of seconds to minutes) but still occur on relatively short time scales (days to years) and almost always have adverse effects. This thesis focuses on eutrophication and its reversal (timescale of days to years) and earthquake events (timescale of seconds to minutes) as examples of the interplay between a decadal anthropogenic stressor and cataclysmic natural events.

Eutrophication

Eutrophication occurs when excess nutrients from terrestrial sources enter the coastal zone (Valiela et al. 1997, Cloern 2001, Diaz and Rosenberg 2008). Increased nutrient levels lead to increased production of particulate and dissolved organic matter that becomes degraded and causes lowered oxygen concentrations (Diaz and Rosenberg 1995). Historically, many coastal ecosystems have been influenced by eutrophication but it is only recently that this phenomenon has become recognised as widespread and subjected to detailed scientific investigation (Wulff et al. 1990, Nixon 1995). Although the magnitude of the problem varies significantly among regions, eutrophication is considered to be one of the major threats to today's marine environment (Wulff et al. 1990, Cloern 2001). Nitrogen and phosphorus are the nutrients of most concern in contributing to eutrophication and most commonly enter the marine environment via groundwater, fluvial and atmospheric inputs (Wulff et al. 1990, Nixon 1995, Cloern 2001). Human activities have increased the quantity of sewage inputs and agricultural runoff, increasing the amounts of organic matter and nutrients entering the marine environment (Smith et al. 1999). Sewage generally has high levels of ammonium and phosphorus whereas agricultural inputs are usually high in nitrate. Although nitrogen and phosphorus are required for growth and production, large quantities can have detrimental impacts on the structure and functioning of marine ecosystems.

Increased nutrient levels from wastewater and terrestrial runoff can cause excessive amounts of primary production, respiration and the generation of particulate matter. This can lead to severely degraded sediment chemistry, suboxic and anoxic water and sedimentary habitats for biota, blooms of nuisance macroalgae, toxic phytoplankton blooms, reductions in faunal diversity and changes in food web structure (Nixon 1995, Paerl 1997, Smith et al. 1999, Cloern 2001, Savage et al. 2002, Lapointe et al. 2005). The extent of these impacts and their consequences depend both on the type (e.g., sewage effluent, agricultural runoff, fertilisers, stormwater) and quantity of the input, as well as the characteristics of the environment to which it enters (e.g., hydrodynamics, hydrography, flux, mineralization and burial rates) (Cloern 2001).

New Zealand has numerous areas with excessive catchment-derived nutrient inputs arising from rivers, drains and industrial and municipal wastewater plants that put large volumes of nutrient-rich runoff and wastewater into the shallow coastal

zone, particularly estuaries. These include Manukau and Tauranga Harbours, Orakei Basin (Auckland), Whangmata Estuary, Moutere Inlet (Nelson), Ahuriri Estuary (Napier), Titahi Bay (Wellington) and the Avon-Heathcote/Ihutai estuarine system (Christchurch). The costs to remediate these impacts are large (often greater than $100 million) but surprisingly, there are few models or case studies of the consequences of "turning off the tap" with which to judge the costs versus benefits of nutrient-input reduction in such systems (examples include Orbetello Lagoon, Italy (Lardicci et al. 2001), Golden Horn Estuary, Istanbul (Yuksek et al. 2006), Mondego Estuary, Portugal (Grilo et al. 2009), Isle of Bute, Scotland (Moore and Rodger 1991), Ems Estuary, border of the Netherlands and Germany (Essink 2003), Victoria Harbour, Hong Kong (Cheung et al. 2008), Laajalahti, Finland (Kauppila et al. 2005), and Moa Point, Wellington NZ (Rogers 1999)). Instead, it has been more usual to study such systems as they become increasingly affected by multiple stresses, but these shed little light on the reverse processes.

Earthquakes

Large earthquakes are unpredictable events that occur infrequently and rapidly, often in remote or offshore locations where it is impractical to study their ecological effects. Consequently it is not surprising that there are very few studies reporting the ecological impact of earthquakes on populations or communities. Those studies that have been done have occurred across a wide range of systems, including forests (Wells et al. 2001), streams and rivers (Fang et al. 2002, Lai et al. 2007) and rocky shores (Castilla 1988). The only known study examining earthquake impacts on communities in an estuarine system is by Maa et al. (2006) who reported the impacts of earthquakes in 1999 and 2002 on insect communities in estuarine mangroves in northern Taiwan.

1.2. Effects of large-scale change on the structure and functioning of marine communities

Disturbance and stress can alter the structure and functioning of marine ecosystems. They can cause reductions in biodiversity not only with regards to species richness, but they can also have adverse effects on functional diversity, species abundance, biomass and evenness (Chapin et al. 1997). Such changes are due to differences among species in their sensitivities to environmental stress that result in a non-

random loss of species (Smith and Knapp 2003, Gonzalez and Loreau 2009). This can occur via direct (e.g., smothering, toxic poisoning) and/or indirect (e.g., changes in oxygen and/or nitrogen concentrations, light attenuation, turbidity, food supply, trophic relationships) pathways (Gearing et al. 1991).

Ecological theory predicts that biodiversity is at its lowest immediately after a disturbance and that post-disturbance diversity will generally increase for a period of time until a natural "equilibrium community" is reached (intermediate disturbance hypothesis, described by Connell (1978)). The trajectory of recovery between the initial post-disturbance and the "final" equilibrium community varies among ecosystems and depends on many factors including the type, intensity and scale of the disturbance, species life histories and current and wind dynamics. A number of models have been developed to describe disturbance-recovery dynamics (for example, models by Grassle and Sanders 1973, Grime 1973, Johnson 1973, Osman 1977, Pearson and Rosenberg 1978, Huston 1979, Warwick 1986, Connell 1987). These models are discussed in *Chapter 2* but are generally variations on that developed by Pearson and Rosenberg (1978) which describes that with increasing organic matter, a "normal community" with diverse fauna (predominately k-selected) changes to a "transitional community" with increased numbers of opportunistic (r-selected) species. A peak in the arrival of opportunistic species occurs at medium to high levels of organic matter, and as very high levels are reached, macrobenthic species disappear. Not only can disturbance change the structure of communities, but it can also alter trophic relationships and entire food webs. This can occur through alterations in the flux of energy and materials or by changes in the abundances of species that control these fluxes such as where the removal or extinction of a particular species results in the explosion of another species and the subsequent depletion of a particular food source. A well-known example of this is where the removal of sea otters caused a massive increase in sea urchins that in turn caused a dramatic reduction in kelp forest due to increased grazing pressure (Estes and Palmisan 1974).

It is generally supported that increased biodiversity promotes the increased functionality and stability of ecosystems and these can enhance ecosystem services (Tilman et al. 2006, Naeem 2009). Consequently, reductions in biodiversity after a disturbance may decrease the functioning and services of the ecosystem. Ecosystem functioning is affected by biotic and abiotic factors and there are many

processes that contribute to, and can be used to define, the functioning of ecosystems. These include primary production, the flux and uptake of nutrients, biomass accumulation and decomposition rates. Of these, primary production is probably the most widely measured (Schwartz et al. 2000). Despite the consensus that losses of biodiversity adversely affect ecosystem functioning, there is some debate regarding the mechanisms by which this occurs (Loreau and Hector 2001). One hypothesis is that particular species that are lost from an ecosystem may be substituted and compensated for by another species ("redundancy hypothesis") although the likelihood of this occurring in natural systems is debated (Loreau 2004). The "rivet hypothesis" argues that each species makes a unique contribution to the ecosystem and therefore its function cannot be substituted or compensated for by another species. It may also be that the effects of species loss on ecosystem functioning do not occur in a predictable fashion, but rather are specific to individual scenarios (Lawton 1994, Peterson et al. 1998, Naeem 2002, Schiel 2006).

1.3. Ecosystem resilience and recovery

The resilience of an ecosystem can be defined as how well it can absorb disturbance and continue to function when faced with a disturbance or environmental change (Holling 1973, Berkes 2003). Sterk et al. (2013) considered resilience to be influenced by ecosystem resistance (i.e., how much change can be absorbed by the ecosystem without altering its functioning), and ecosystem recovery (i.e., how quickly the ecosystem will return to its previous condition). These factors will greatly influence the extent to which biodiversity is altered. In less resilient systems, mortality and reductions in biodiversity may occur directly from the disturbance. In more resilient systems, biodiversity may not be affected or may be altered indirectly, via the impacts of the disturbance on the physiological tolerances, behaviour, growth, activity patterns, distribution, reproductive output and immunity of populations (Newell 1979, Beardall et al. 1998, Harvell et al. 1999). The diversity–stability hypothesis (McNaughton 1977) proposes that resilience is higher in more species-rich communities because there is a greater diversity of species responses when faced with disturbance.

The recovery of the marine environment from slow and abrupt changes may follow different time scales and trajectories, depending on the event responsible for the change. Sometimes recovery can occur rapidly after the cessation of the

disturbance but this depends on the scale of the disturbance, its intensity and perhaps most importantly, the species involved (Thompson et al. 2002). Generally, populations of fast-growing species recover quicker than those with slow-growing species. The speed of recovery is also increased in areas exposed to larvae or propogules from nearby unaffected populations that can aid recruitment. Organisms that have direct development have been observed to recover more slowly than those with indirect development because the rate at which organisms from other areas reach the disturbed area is much lower (Gibbs et al. 1991, Watt et al. 1993).

For an ecosystem to recover, it must in principle return to a previous condition of increased ecological health where the community will have similar species composition, population density, size and biomass to that of the historical baseline ecosystem (Elliott et al. 2007). In practice, this definition is not always workable because historical conditions are not always known and it can be difficult to assess what constitutes natural and pristine conditions. Furthermore, the impacts of some disturbances are irreversible, for example where there are introductions of non-native species (Thompson et al. 2002) or where there are permanent physical changes to the ecosystem (e.g., Lebednik 1973). Sometimes the disturbance may cause a community to shift to an alternative stable state that may persist even after the disturbance is removed. In many cases this may represent an improved natural alternative to the historical state (Simenstad et al. 2006).

1.4. Estuarine ecosystems

An estuary can be described as “a partially enclosed body of water that is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixing of sea water with fresh water derived from land drainage” (Day 1980). Estuarine ecosystems are critical transition zones where inputs of energy and matter from terrestrial, freshwater and marine environments are processed and transformed (Ketchum 1983) and can include habitats of rocky outcrops, sand dunes, mangroves and salt marshes (Day 1981, Raffaelli 1992). Estuaries provide highly important feeding and nursery grounds for juvenile fish and bird species, and support a high diversity of flora and fauna including macro- and micro- algae, bacteria, seagrass, mangroves, phytoplankton, zooplankton, infauna, epifauna, fish and birds (Knox 1973, Owen 1992).

Morphologically, estuaries are highly influenced by their location, wind, wave and tidal action, hydrology, erosion and, on a larger scale, tectonic activity (Dyer 1979, Day 1981, Mclusky 1981, Perillo 1995). The structure and functioning of estuarine ecosystems is often affected by anthropogenic activities and this has resulted in the severe degradation of many estuaries worldwide (Robertson 2002). This is due in part to the rapid expansion of worldwide coastal populations in recent years, with more than six billion people expected to live in coastal areas by 2025 (Schwartz 2005). This places significant pressures on estuarine habitats, including overexploitation by recreational and commercial fisheries, increased eutrophication and sewage inputs, habitat loss and alteration through development, increased input of chemical contaminants, increased risk of introduced species, increased input of debris/litter and an increased risk of sea level rise (Nixon 1995, Cloern 2001). In turn, these stressors have negative consequences for the ecosystem, including loss of habitats and diversity, algal blooms, increased primary production, increased organic matter and hypoxic/anoxic conditions (Hull 1987, Paerl 1997). These not only have a direct effect on the ecosystem but can also have significant indirect effects on the recreational, aesthetic and commercial value of the estuary.

In New Zealand, there are around 300 estuaries (Mclay 1976) that have been classified into five groups, based on the processes that shaped their basin, and a further 16 classes, based on their morphological features (Hume 1988). The major groups are estuaries originating from 1) fluvial erosion, 2) marine/fluvial erosion, 3) tectonism, 4) volcanism, and 5) glaciation. The Avon-Heathcote Estuary, the focus of this thesis, was formed through fluvial erosion. More details are available in Hume (1988).

1.5. Objectives and aims

The original aim of this thesis was to examine estuarine invertebrate responses to large-scale change associated with the reversal of eutrophication resulting from the diversion of wastewater to an ocean outfall. This expanded considerably into understanding the added effects of several earthquakes, which occurred approximately one year into my study. Large-scale change refers to significant alterations in the physical, chemical and/or biological environment that, in this case, occurred as a consequence of 1) the diversion of wastewater offshore to an ocean outfall (reversal of eutrophication), and 2) cataclysmic earthquake events (abrupt

disturbance) in Christchurch's Avon-Heathcote Estuary. This research aimed to address three key questions, using field and laboratory settings and a wide range of spatial and temporal scales including a spatial gradient of eutrophication.

1) How do estuarine invertebrate communities and their habitats respond to large-scale change?

   Hypothesis #1: Invertebrate communities in eutrophic and highly disturbed areas would have a lower taxa richness and a higher portion of opportunistic species

   Hypothesis #2: Habitats in eutrophic areas would have more cohesive sediments with higher amounts of organic matter, legacy nutrients and pollutants

   Hypothesis #3: Liquefaction mounds ("new" sediments produced by the earthquakes) would be coarser, less organic-rich and have fewer pollutants and nutrients than the surrounding "old" sediments. In new sediments, taxa richness and the abundance of both infauna and surface fauna were expected to be low initially (with initial populations dominated by opportunistic species) and then increase over time, due to colonisation by fauna in neighbouring old sediments, until an equilibrium was reached.

2) What are the impacts of large-scale change on estuarine invertebrate food webs?

   Hypothesis #1: Food sources and consumers from eutrophic areas would have $\delta^{13}C$ and $\delta^{15}N$ isotopic values that were more depleted (lower) than food sources and consumers in less eutrophic areas. This would be driven by a higher uptake of depleted sewage-derived carbon and nitrogen by the primary producers in eutrophic areas that would then passed on to consumer organisms.

   Hypothesis #2: Spatial differences in the isotopic values of food sources and consumers would decrease after the diversion due to the cessation of sewage inputs to the estuary.

   Hypothesis #3: Isotopic values of food sources and consumers would become more depleted after the earthquakes due to the uptake of raw sewage by primary producers, and in turn, consumers.

3) How is ecosystem functioning, and the role of invertebrates in this process, affected by large-scale change?

   Hypothesis #1: Nutrient (especially NH_4-N) efflux would be greater in old sediments than in new sediments after the earthquake. The capping of eutrophic old sediments with clean new sediments was expected to reduce nutrient release. As old and new sediments mixed over time, I expected levels of nutrient efflux to become more similar between the two sediment types.

Hypothesis #2: Gross primary production (GPP) would be greatest in old sediments as these sediments appeared, visually, to have a higher biomass of BMA. This assumed a positive correlation between GPP and BMA biomass. But, I also expected this to be driven by greater nutrient (especially NH_4-N) release in old sediments (nutrients are a requirement of photosynthesis and NH_4-N is the most readily utilisable form of nitrogen).

Hypothesis #3: The addition of Amphibola, a surface grazer, would reduce BMA biomass and consequently levels of GPP in old and new sediments. Nutrient flux in this treatment was not expected to differ greatly from the control.

Hypothesis #4: As Austrovenus occurs mainly beneath the sediment surface and can bulldoze surface sediments, I expected NH_4-N efflux in this treatment to be higher than in the control treatment. I expected GPP to be similar or slightly elevated relative to the control.

Hypothesis #5: Austrohelice treatments would show reduced levels of GPP. This would be attributable to both the consumption of BMA and its burial from bioturbation.

Chapter 2: Examines the effects of the reversal of eutrophication (wastewater diversion) and earthquake events on estuarine communities and habitats. This chapter includes a two-and-a-half year dataset that encompasses pre-diversion/post-diversion and pre-earthquake/post-earthquake sampling periods. Changes in infaunal and surface faunal communities, algal cover and biomass, and sediment composition are examined over wide spatial scales that encompass a eutrophication gradient.

Chapter 3: Focuses specifically on earthquake-driven changes to the Avon-Heathcote Estuary. Here, the effects of the earthquakes on the physical and chemical environment and their impacts on invertebrate and marine plant communities are examined. This is achieved by comparing new (earthquake-introduced liquefaction mounds) and old (adjacent non-impacted) sediments across spatial and temporal scales.

Chapter 4: Describes spatial and temporal changes in the pathways of carbon and nitrogen flow through an estuarine food web in response to large-scale change. A two-and-a-half year dataset of $\delta^{13}C$ and $\delta^{15}N$ values of food source and consumer organisms within the Avon-Heathcote Estuary is analysed over a range of spatial scales encompassing a eutrophication gradient. Trophic relationships and individual species shifts are examined in relation to the diversion and earthquake events.

Chapter 5: Uses *in situ* and laboratory-based experiments to investigate earthquake-driven effects on ecosystem functioning. Specifically, the effects of sediment type and invertebrate functional guild on primary production and nutrient flux are examined in the context of changes to the ecosystem resulting from disturbance.

Chapter 6: Presents an overall synthesis and general discussion of the impacts of large-scale change on estuarine communities and their environments. Implications for management are discussed.

1.6. Study site

The Avon-Heathcote Estuary/Ihutai

The Avon-Heathcote Estuary/Ihutai, located in Christchurch New Zealand (43^{o} 33' S, 172^{o} 44' E), is a shallow (average depth 1.4m), roughly triangular-shaped estuary enclosing an area of approximately 8km^{2} (Knox 1973) (Fig. 1.1). The estuary is fed by two slow-flowing rivers: the Avon in the northern corner, and the Heathcote in the south-west. Both rivers flow through residential areas, with the Avon River passing through commercial and rural areas and the Heathcote passing through more industrial areas. The estuary mouth is situated in the south-east corner, between the end of Brighton Spit and Moncks Bay. The total catchment area of the estuary is approximately 190km^{2} (Bolton-Richie 2005) with around 8.5 x 10^{6} litres of sea water entering on each mean flood tide. Approximately 8.3 x 10^{6} m^{3} of the total salt and fresh water inflow is removed from the estuary with each outgoing tide (Knox 1973). Tides are semi-diurnal, dominated by wind and wave action and have a maximum range from 1.7 (neap tide) to 2.2m (spring tide). Due to the shallow depth and tide and wind action, the estuary is generally well-mixed (Knox 1973) but salinity can vary considerably depending on the positioning of areas in relation to the rivers and estuary mouth. Bolton-Richie (2008) found salinity to range from 10.2 to 33.7‰ at different sites throughout the estuary during high tide.

The dominant habitat (~85%: Stephenson (1981)) in the Avon-Heathcote Estuary is intertidal sand and mudflats and these support a diverse community of birds (e.g., pied oystercatcher, geese, swans, shoveler, grey teal, ducks, oystercatchers, godwits, dotterels, plovers, pied stilts, herons, royal spoonbill) and a large range of marine organisms such as flounder and other small fish, mud-snails, crabs, whelks, cockles and worms (Owen 1992). Wetlands situated at the mouth of

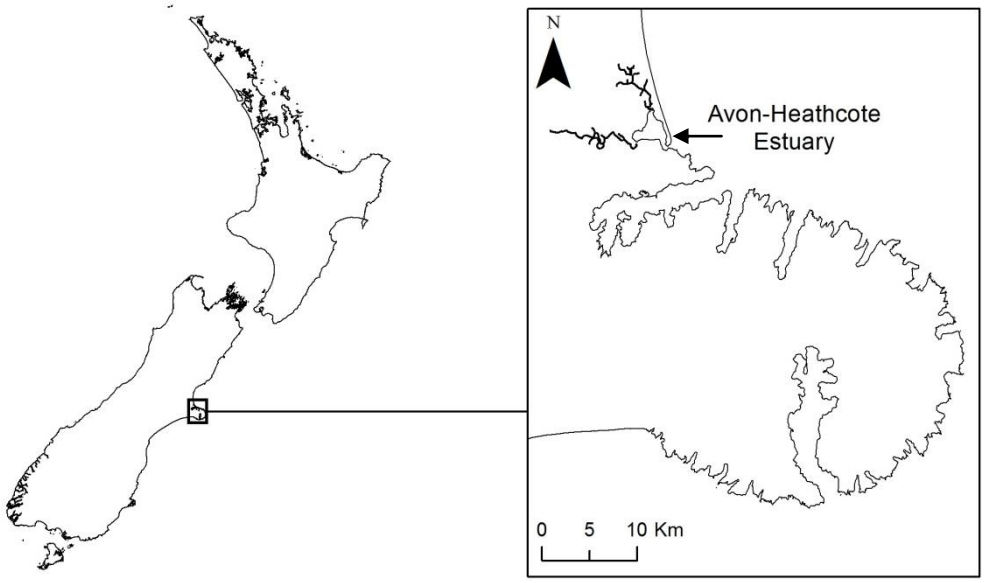

Figure 1.1. Location of the Avon-Heathcote Estuary in Christchurch New Zealand.

the Avon River at the head of the estuary provide important habitat for raupo (reeds) and other plants, with mat/turf-forming vegetation occurring nearer the estuary shore and algae (macro-/micro-) growing within the estuary. The dominant macroalga is the green sea lettuce *Ulva* spp.. This complex is composed of the frondose form *Ulva lactuca*, the tubular form *Ulva* (formerly *Enteromorpha*) *intestinalis* and the hollow compressed form *Ulva* (formerly *Enteromorpha*) *compressa*. The red alga *Gracilaria chilensis* can also exhibit high biomass in some areas (Bolton-Richie 2011). There are some areas of seagrass (*Zostera muelleri*) occurring on the eastern side of the estuary near the estuary mouth. In addition to these biological characteristics, the estuary offers open space for recreational activities such as kiteboarding, kayaking, windsurfing, walking, bird-watching and picnicing (Owen 1992, Bolton-Richie 2005).

Wastewater Input and Diversion

In 1882, a sewage farm was constructed in response to population pressures, to release untreated sewage (from septic tanks) from the surrounding community into the Avon-Heathcote Estuary (Bolton-Richie 2005). In 1962, a tertiary treatment system was introduced, incorporating settling tanks, trickling filters and biological oxidation in a series of ponds (Knox 1973, Owen 1992). This new infrastructure was completed in 1971 and had subsequent upgrades in 1978, 1996 and 2004 (Knox 1973, Bolton-Richie 2005). Prior to 1973, discharge of treated effluent to the estuary

was continuous but since then it has occurred diurnally on the ebb tide. From October 2003 to February 2010, up to 500,000m^3/day of effluent was discharged into the estuary at a maximum rate of 17.4m^3/s for four hours (one hour before and three hours after high tide) in each tidal cycle (URS 2004). Bolton-Richie (2005) reports that the wastewater contributed 90% to 98% of the total nitrogen and phosphorus inputs into the estuary during this period. Additional nutrients and other pollutants such as heavy metals, chemicals, urban runoff and stormwater enter the estuary via the Avon and Heathcote Rivers (Knox 1973, Owen 1992, Robertson 2002).

In March 2010, the Avon-Heathcote estuary experienced a large (~90%) reduction in nutrient loading due to the diversion of wastewater to an ocean outfall, extending 3km offshore from South Brighton Beach. This diversion was one of the largest and most expensive (~$89 million) ever done in New Zealand and was expected to initiate a major ecological recovery to this highly eutrophic estuary.

Canterbury Earthquakes

Between 4 September 2010 and 10 January 2012, 3149 earthquakes and aftershocks of magnitude 3 or greater occurred in Canterbury New Zealand as a result of the grinding of the Australian and Pacific tectonic plates (Geonet 2011). Four large earthquakes occurred during this time period: 4 September 2010 (magnitude 7.1), 22 February 2011 (magnitude 6.3), 13 June 2011 (magnitude 6.3) and 23 December 2011 (magnitude 6.0).

The February and June 2011 earthquakes caused considerable damage to the estuary, causing widespread liquefaction and destruction of sewage pipes causing large quantities of untreated sewage to enter the estuary. During the February earthquake, the estuary floor was tilted with the northern side subsiding by 0.2-0.5m and the southern side rising by 0.3-0.5m (Measures et al. 2011). More details of these earthquakes and their impacts on the estuary are presented in *Chapter 3*.

Liquefaction

Visually, one of the most obvious impacts of the earthquakes on the Avon-Heathcote Estuary was the appearance of large mound-like structures on the surface of the estuary (Fig. 1.2). These mounds, that throughout this thesis are referred to as “new sediments,” were from liquefaction that occurred as a result of the February and

June 2011 earthquakes. Liquefaction occurs when a granular material such as soil or sediment transforms from a solid to a liquefied state due to increased pore-water pressure (Marcuson 1978). During an earthquake, the rapid shaking action causes soil or sediment particles to rearrange themselves, become more compact and weakening the contact forces between them (Morris 1983). This can cause liquefied sand and water, from several metres deep to force its way to the surface. This liquefied material is often observed as “sand volcanoes” or “sand boils” that occur on the surface and most commonly occur in poorly compacted sandy or silty areas below the water table (Morris 1983).

Figure 1.2. Liquefaction in the Avon-Heathcote Estuary after the 2011 Earthquakes.

Study sites

The main eight study sites used throughout this study are shown in Fig. 1.3. These sites were chosen at least partially because they were part of a wider program and there was a history of work at these sites (by the National Institute of Water and Atmospheric Research (NIWA)) prior to my study. However, they were also selected because they encompassed a gradient of eutrophication. This included highly eutrophic sites (Humphreys and Discharge), river sites with some eutrophication (Avon and Heathcote) and relatively clean sites (Heron, Heron 2, Plover and Pukeko). Site characteristics are given in Table 1.1. The eutrophic sites are situated in a low-flow "back-water" area on the south-western side of the estuary. Historically, these sites have received high nitrogen and organic loading due to their proximity to the former discharge pipe and the low current velocity and circulation in this area. Prior to March 2010, this pipe discharged up to 500,000m^3 of wastewater into the estuary daily from the Bromley Oxidation Ponds (URS 2004).

Table 1.1. Relative characteristics of the main study sites in the Avon-Heathcote Estuary pre- and post-earthquake.

	Pre-Earthquake			Post-Earthquake	
Site	**Eutrophication Gradient**	**Tidal Flows**	**Salinity**	**Tilting of Estuary Floor**	**Amount of Liquefaction**
Humphreys	▲ Highest	Lowest	High	+0.3-0.4	High
Discharge	High	Low	High	+0.2-0.3	Some
Heathcote	Some	Some	Low[1]	+>0.5	High
Avon	Some	Some	Low[2]	-0.1-0.2	Some
Heron	Low	High	High	+0.05-0.1	Low
Heron 2	Low	High	High	+0.05-0.1	Low
Plover	Low	High	High	+0.1-0.2	High
Pukeko	Lowest	▼ Highest	High	+0.2-0.3	Low

[1]1.2-16‰ during a tidal cycle (Bolton-Richie 2011)
[2]12-25.9‰ at high tide (Bolton-Richie 2011)

The river sites are situated in the estuary at their respective river mouths. Avon is at the northern end of the estuary and Heathcote at the southern end. Due to their locations, they are exposed to high amounts of riverine freshwater inputs. Nutrients, storm-water run-off, heavy metals and other pollutants can also enter the estuary via these rivers (Knox 1973). After the earthquakes, sewage and wastewater entered the estuary via the Avon and Heathcote Rivers.

The least eutrophic ("clean") sites are situated on the eastern side of the estuary closest to the estuary mouth where they are more influenced by marine

processes. The sediments and channels at these sites, particularly at Pukeko the least eutrophic site, are the most dynamic of all sites. Note that 1) after the February 2011 earthquake, large quantities of raw sewage entered the estuary via a culvert that flowed onto the sampling area at Plover St until November 2011, and 2) Heron 2 occurs slightly south of Heron but in the mid-low shore zone. This site was chosen due to the presence of seagrass (*Zostera muelleri*).

Additional sampling sites, used for the collection of fish species for isotopic analysis in *Chapter 4*, are shown in Fig. 1.4.

Figure 1.3. Study sites (red squares) and other notable locations (blue squares) in the Avon-Heathcote Estuary.

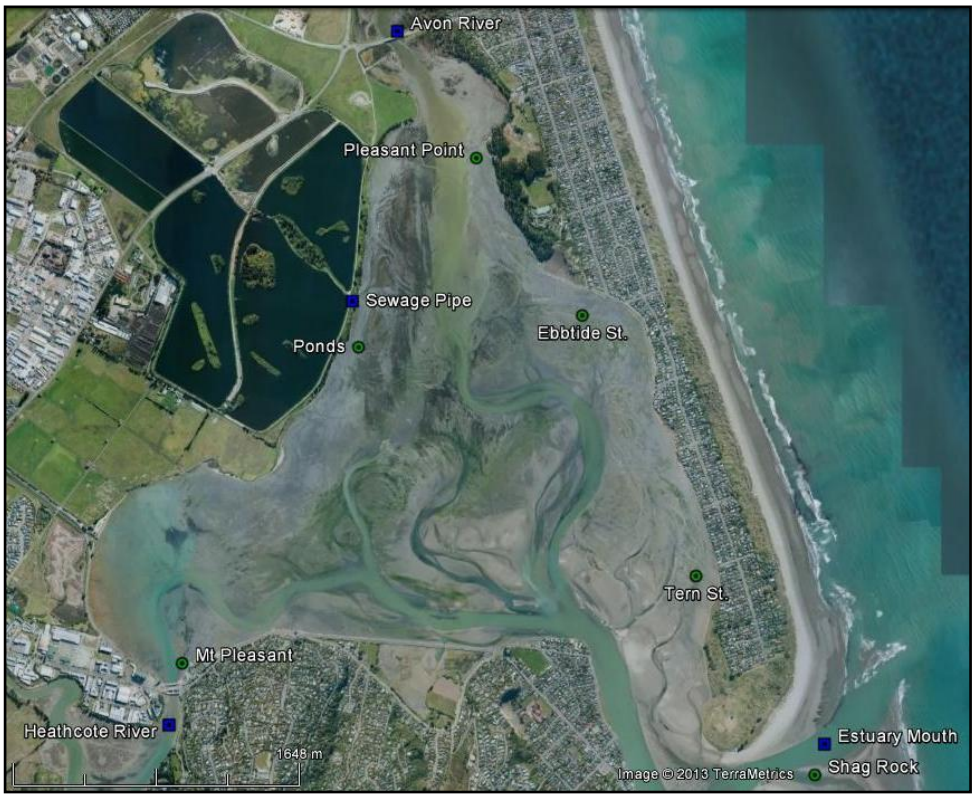

Figure 1.4. Additional sampling sites (green circles) used for the collection of fish species for isotopic analysis in *Chapter 4*. Other notable locations are indicated by blue squares.

1.7. Key study species

1.7.1. Macroinvertebrates

Austrovenus stutchburyi (Fig. 1.5A)

Austrovenus stutchburyi (Wood 1828) is an infaunal suspension feeding venerid bivalve that is endemic to New Zealand and found in the surface sediments of intertidal mud and sandflats (Morton 1968). This species is common in estuaries throughout New Zealand where it can occur in densities of up to ~1800m^{-2}. Individuals can grow in excess of 30mm in length and can live for up to 20 years (Morton 1973, Dobbinson 1989, Whitlatch et al. 1997). This species has a pelagic larval phase of two to three weeks during which it is capable of dispersing over relatively long distances (Stephenson and Chanley 1979, Ross et al. 2012). Ecologically, *Austrovenus* plays an important role in reworking sediments in the top 2-3cm and can significantly influence the biogeochemical flux of oxygen and nutrients in New Zealand estuaries (e.g., Sandwell et al. 2009, Jones et al. 2011).

Amphibola crenata (Fig. 1.5B)

Amphibola crenata (Gmelin 1791) is a pulmonate gastropod endemic to New Zealand (Little et al. 1985). Larvae of this species spend several weeks at sea before settling in the upper reaches of estuaries and other soft sediment habitats (Pilkington and Pilkington 1982). Adults can be abundant on both mud and sand flats in inlet, estuarine, salt marsh and mangrove habitats where they deposit feed on exposed sediment surface organic matter during low tide. Ingested particles that are unable to be digested are egested; forming a continuous faecal string of mucus bound particles that trail behind the mud-snail (Juniper 1987).

Austrohelice crassa (Fig. 1.5C)

Austrohelice crassa (cf. *Helice crassa*, Dana 1852) is a highly mobile grapsid crab that builds extensive burrow networks (up to 60cm deep) in New Zealand's soft sediment environments (Beer 1959, Guerra-Bobo and Brough 2011). It is commonly found in high abundances in mudflats where up to 462 individuals per m^2 (Jones and Simons 1983) can occur at mid-to-high shore. *Austrohelice* is a relatively small crab (adult carapace width ~2cm (Beer 1959)) but is an avid bioturbator and plays an

important ecological role in soft-sediment ecosystems (Kristensen 2008, Needham et al. 2010).

Macrophthalmus hirtipes (Fig. 1.5D)

Macrophthalmus hirtipes (Heller 1862) is a mud crab that is endemic to New Zealand where it occurs in the mid-to-low shore zone of soft-sediment environments (Woods and Schiel 1997). This species is a deposit feeder (Beer 1959) that builds temporary burrows in water-logged areas. It has been found to be unable to tolerate salinities below 4‰ (Jones 1982).

Hemigrapsus crenulatus (Fig. 1.5E)

Hemigrapsus crenulatus (Milne Edwards 1837) is a mid-to-high shore crab native to New Zealand but also found on the Chilean coast (Retamal 2000, Urbina et al. 2010). This species is usually found in estuarine habitats burrowed in sand, mud or living under stones (Morton 1968). This species can occur in high densities (up to 10 individuals per m^2 (Pulgar et al. 1995)) and is sexually dimorphic (Diaz-Jaramillo et al. 2013).

Figure 1.5. Key invertebrate study species in the Avon-Heathcote Estuary: *Austrovenus stutchburyi* (A), *Amphibola crenata* (B), *Austrohelice crassa* (C), *Macrophthalmus hirtipes* (D) and *Hemigrapsus crenulatus* (E).

1.7.2. Marine plants

Benthic microalgae (BMA) (Fig. 1.6A)

Benthic microalgae are microscopic unicellular protists that occur in the top few millimetres of sediments in soft-sediment environments, particularly estuaries (Graham 2000). These microalgae are important primary producers in such shallow water environments and in estuaries, it has been estimated that they can account for >50% of primary production (Underwood and Kromkamp 1999). Benthic microalgae can increase the cohesiveness of surface sediments and play an important role in influencing both the microenvironment and ecosystem functioning through the

uptake of sediment and water-column nutrients. They can use these nutrients to assist with growth and primary production under light conditions (Lorenzen et al. 1998). Hutt (2012) found BMA taxa from four divisions in the Avon-Heathcote Estuary: Chrysophyta (golden algae), Chlorophyta (green algae), Euglenophyta (flagellates) and Cyanophyta (blue-green bacteria).

Gracilaria chilensis (Fig. 1.6B)

Gracilaria chilensis is a red alga (Rhodophyta) usually found in protected shallow marine waters and estuaries (Gomez et al. 2005). This species is found throughout New Zealand but was originally described from Chile (Bird et al. 1990, Candia et al. 1999). Species from this genus have been widely used for the extraction of agar and as food for aquaculture (Schiel and Nelson 1990, Hurd et al. 2004).

Ulva spp. (Fig. 1.6C)

Ulva (Linnaeus 1973) is a genus of green alga (Chlorophyta) with thalli divided into elongated segments (Adams 1994). *Ulva* and *Enteromorpha* are morphologically distinct but recent DNA evidence has grouped them within the genus *Ulva* (Hayden et al. 2003). There are three species of *Ulva* in the Avon-Heathcote Estuary: *Ulva lactuca*, *Ulva* (formerly *Enteromorpha*) *intestinalis* and *Ulva* (formerly *Enteromorpha*) *compressa*). *Ulva lactuca,* commonly known as sea lettuce, has thin cellophane-like fronds that appear as green translucent sheets. In comparison, *Ulva intestinalis* has thin, tubular filaments with thalli consisting of a monostromatic layer (as opposed to *Ulva lactuca* whose thalli are distromatic) (Barr 2007). *Ulva compressa* has elongated compressed hollow fronds. Unless otherwise stated, throughout this thesis "*Ulva spp.*" and "*Ulva*" are used to include all species within this genus occurring in the estuary (although the majority of this is *Ulva lactuca)*. *Ulva* is commonly found in intertidal and estuarine habitats but can also occur on exposed coastlines (Adams 1994, Blomster et al. 1998). It is a fast-growing and opportunistic macroalgae that can exhibit high rates of nitrogen uptake and proliferate under high nutrient conditions (Blomster et al. 1998, Taylor and Rees 1999).

Zostera muelleri (Fig. 1.6D)

The seagrass *Zostera muelleri* (Irmisch ex Asch.), is a monoecious marine angiosperm that occurs in New Zealand and along the east coast of Australia (Jones

et al. 2008). It has formerly been referred to as *Zostera novazelandica* but phylogenetic analysis has shown little morphological and molecular variation between the two species (Les et al. 2002). *Zostera* reproduces both sexually and vegetatively and usually occurs in sheltered intertidal soft-sediment areas such as estuaries and bays (Inglis 2003). This species plays an important role in stabilising sediments, reducing water movement, providing habitat for invertebrates, structuring benthic communities and influencing ecosystem functioning due to high productivity (Edgar and Shaw 1995, Irlandi and Crawford 1997, Turner et al. 1999, van Houte-Howes et al. 2004). *Zostera* is, however, sensitive to pollution, sedimentation, disturbance and other changes in the physical environment (Bearlin et al. 1999).

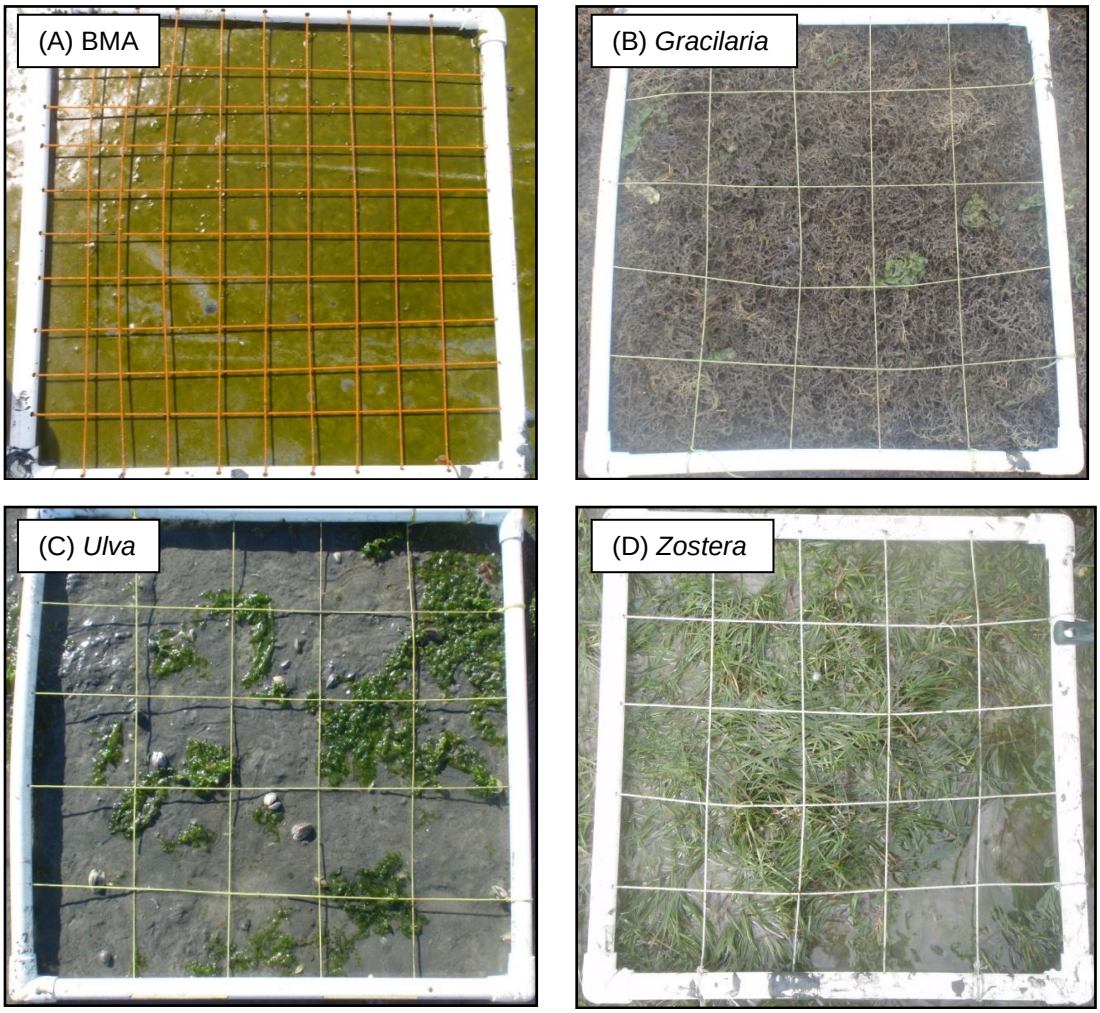

Figure 1.6. Key marine plant species in the Avon-Heathcote Estuary: Benthic microalgae (BMA) (A), *Gracilaria chilensis* (B), *Ulva* spp. (C) and *Zostera muelleri* (D). Quadrat size is 0.5 x 0.5m.

Chapter Two

Estuarine Habitats and Communities:
Spatial and Temporal Changes in Response to Eutrophication and Disturbance

2.1. Introduction

Estuaries are highly variable ecosystems exposed to a wide range of natural and anthropogenic stressors and disturbances (Posey 1990, Elliott and Quintino 2007). Natural stressors can include seasonal cycles of temperature, light and freshwater inputs. Common forms of anthropogenic stress are the exploitation of estuarine resources and chronic eutrophication, which occurs when excess nutrients from terrestrial sources enter coastal waters (Valiela et al. 1997, Cloern 2001, Elliott and Quintino 2007, Diaz and Rosenberg 2008). Disturbances, on the other hand are often relatively quick and discrete events that disrupt ecological communities either directly or through the alteration of habitats and resources (White 1985). These include extremes of sediment and nutrient runoff, storms, and direct human impacts such as land reclamation. Natural and human disturbances and/or stressors occur simultaneously and their interactive effects can affect habitats and communities in synergistic ways, not necessarily additive (Hobbs and Huenneke 1992). Overall effects can include changes in ecosystem energetics (e.g., increased respiration, increased levels of production/respiration per biomass), nutrient cycling (e.g., increased turnover of nutrients, increased horizontal transport), and community structure (e.g., shorter lifespans, reductions in the size of organisms, more r-strategists) (Odum 1985). Furthermore, the effects of stress and disturbance on biota can be detected not only at community and population levels, but also physiologically (Elliott and Quintino 2007).

Environmental impact assessments in estuarine environments usually focus on describing the structure of communities through time, often in comparison to a baseline level. This can involve monitoring changes in flora, for example increases in the biomass of opportunistic algae such as *Ulva* spp. after nutrient enrichment (Wilkinson 1995), or changes to infaunal benthic communities, which can be good indicators of environmental conditions. Generally, methods involve quantifying variables such as species abundances, richness and biomass and that enables calculation of various diversity and evenness indices and ratios (Elliott and Quintino 2007).

Many models have been developed to predict the effects of disturbances and stressors on resident biota. Perhaps the best known model is that created by Pearson and Rosenberg (1978) that examined the effects of disturbance and stress on benthic organisms by modelling changes in the number of species, abundances

and biomass along a gradient of increasing organic matter content. These authors found that with increasing organic matter, a “normal community” with diverse fauna (predominately k-selected, competitive) changed to a “transitional community,” with increased numbers of opportunistic species (r-selected). A peak in the arrival of opportunistic species occurred at medium to high levels of organic matter, and as very high levels were reached and the sediment became azoic, macrobenthic species disappeared. Many authors have since supported and extended this early work. For example, Warwick (1986) examined relationships between community change and eutrophication and found the shift in community equilibrium resulting from nutrient enrichment was due to the rate of damage being greater than the rate of community recovery. Similar to Pearson and Rosenberg’s model, Warwick (1986) also found an increase in the abundance and biomass of opportunistic species with increased disturbance, and in intensely disturbed environments, total community collapse. This pattern can be explained by the new, unused habitats and resources being created with increasing disturbance which are beneficial for growth and reproduction, thus causing rapid population expansion in r-selected organisms capable of survival in such habitats.

Another well-supported model used to describe disturbance-community relationships is the intermediate disturbance hypothesis (IDH). This can be traced back to work by Eggeling (1947) but was properly described with mechanisms by Grime (1973), Osman (1977) and Connell (1987). The IDH predicts a peak in diversity at intermediate levels of disturbance, due to maximum coexistence between k-selected and r-selected species, and low levels of diversity at both high and low levels of disturbance due to local extinction and competitive exclusion respectively. This model assumes that, in a non-disturbed system, there is a competitive hierarchy of species in which higher competitors are better occupiers of space and eliminate species that are inferior competitors. The IDH has been applied to marine (e.g., Sousa 1979), freshwater (e.g., Padisak 1993) and terrestrial (e.g., Molino and Sabatier 2001) communities and has been supported in laboratory and field environments.

The dynamic-equilibrium model (DEM) developed by Huston (1979) provides a broader range of predictions than the IDH. This model takes into account the rates of productivity (competitive exclusion, population growth) allowing species diversity to peak at low, intermediate or high levels of disturbance. The DEM predicts that at

high levels of productivity, a strong disturbance is required to counteract competitive exclusion. At low productivity levels, a weaker disturbance will prevent competitive exclusion. Maximum diversity is predicted at intermediate levels of productivity (Huston 1979). Similar to the IDM, the DEM has been applied and supported in both aquatic (e.g., Worm et al. 2002, Svensson et al. 2010) and terrestrial (e.g., Turkington et al. 1993) environments.

For all models, the disturbance or stress history of the community of interest must be considered because community resilience increases with repetitive exposure (Dernie et al. 2003). For example, Miller (1982) suggests that small and frequent disturbance events will favour competitive species that grow rapidly, as opposed to large infrequent disturbance events, which will favour coloniser species with a greater dispersal ability. Furthermore, models must take into account the biological mechanisms that can drive community change, such as competition, facilitation, inhibition, tolerance and random colonisation (Whitlatch 1980, Hall et al. 1994). Additionally, some authors argue that biota in highly stressed environments, such as estuaries, may exhibit environmental homeostasis, a resilience that enables them to absorb stress without adverse effects (Elliott and Quintino 2007). Thus it is clear that generalisations are difficult to make and the type and scale of disturbance, as well as the type of species present, must be considered for individual scenarios.

The aim of this chapter was to examine how large scale change, in the form of the reversal of eutrophication and cataclysmic earthquakes, affected the structure of communities and habitats in the Avon-Heathcote Estuary, Christchurch, New Zealand. Specifically, I examined changes in marine plant (algae and seagrass), surface faunal and infaunal communities, and the composition of sediments, across spatial and temporal scales.

From 1973 to March 2010, Christchurch's wastewater was tertiary-treated and discharged diurnally on the ebb tide into the Avon-Heathcote Estuary. Up to 500,000m^3 of wastewater was discharged into the estuary each day (URS 2004). This resulted in some areas of the estuary being highly eutrophic. Because of the point source release of this wastewater, however, there is a eutrophication gradient within the estuary. In March 2010, the treated wastewater was diverted 3km offshore and the estuarine inputs stopped (for full details of the wastewater diversion see *Chapter 1: General Introduction*).

Community and habitat recovery after the diversion was an important part of this study (and indeed the initial focus of my study). Many studies have examined the response of faunal communities to increased nutrient levels, but less is known of their response to nutrient abatement, largely because concomitant faunal and abatement time series are in short supply (Wilson et al. 1998, Savage et al. 2002, Essink 2003). Data on responses of invertebrate communities to nutrient reduction are available for Boston Harbour, where faunal biomass decreased, but diversity increased, within months to years of diversion of wastewater (Taylor 2003). In Valli di Comacchio, northern Adriatic Sea, Italy, the macrobenthic community had still not completely recovered 11 years after the cessation of sewage discharge to the area. This was attributed to limited water circulation, salinity and temperature fluctuations, and the release of toxic substances from the sediment (Munari et al. 2003).

With regards to the diversion of wastewater, I hypothesized that faunal communities would change from having low species richness (with a higher number of a few resilient species), to being more diverse with less skewed abundance patterns. It was, however, expected that changes would not occur immediately (due to the legacy effects of nitrogen in the sediments) and that the magnitude of change would be site-specific depending on the initial levels of eutrophication and baseline communities.

The Avon-Heathcote Estuary was also affected by the Canterbury earthquakes, particularly those that occurred on 22 February 2011 and 13 June 2011. Both of these produced large areas of liquefaction-mounds ("new sediment") and caused significant quantities of raw sewage to enter the estuary from multiple sources until October 2011, because of damaged Christchurch wastewater infrastructure (for full details of the earthquakes see *Chapter 1: General Introduction* and *Chapter 3*). I hypothesised that the effects of the earthquakes would depend largely on the amount of new sediments deposited at each site. At sites where both old and new sediments occurred within the (pre-earthquake determined) transect, I expected there to be considerable within-site variation in sediment and community composition, at the scale of metres.

2.2. Methods

2.2.1. Study sites

Monitoring and sampling were done at seven sites across the Avon-Heathcote Estuary: Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys and Pukeko. A description of each site and a map showing their location is given in *Chapter 1: General Introduction*. Briefly, Discharge is a eutrophic site situated below the former discharge culvert of the Bromley Oxidation Ponds. This was one of the main sites for raw sewage entering the estuary after 22 February 2011. Humphreys is situated in a low-flow "back-water" area about 0.5km from Discharge which also received high amounts of sewage-derived nitrogen post-earthquakes. Because of low tidal flows and circulation at this site, the sediments had historically accumulated high amounts of organic matter and legacy nitrogen (Bolton-Richie 2005). Avon and Heathcote are near their respective river mouths and consequently are exposed to lower salinity and more riverine and terrestrial inputs. Large amounts of wastewater and sewage entered the estuary via these rivers post-earthquakes. Heron, Heron 2 and Pukeko are situated on the eastern side of the estuary (on Brighton Spit) with Pukeko nearer the estuary mouth. The channel and flow patterns within the estuary mean these sites are most influenced by ocean water, among the sites. These were the least eutrophic of all sites before the earthquakes. After 22 February 2011, large quantities of raw sewage entered the estuary at Plover, between the Heron sites and Pukeko, until October 2011. The seven sites can be grouped into three divisions: "eutrophic sites" (Humphreys and Discharge), "clean(est) sites" (Heron, Heron 2 and Pukeko) and "river sites" (Avon and Heathcote). The river sites sit between the eutrophic and clean sites within the eutrophication gradient.

With the exception of Heron 2 (where monitoring occurred in the mid-shore zone), monitoring was done in the high-mid shore zone at each site. Surveys were done on seven sampling occasions (December 2009, February 2010, July 2010, January 2011, July 2011, January 2012 and July 2012) at Discharge, Avon, Heron and Pukeko, on six sampling occasions (February 2010, July 2010, January 2011, July 2011, January 2012 and July 2012) at Heathcote, and on four sampling occasions (December 2009, February 2010, January 2011 and January 2012) at Humphreys and Heron 2.

As detailed in the *Introduction*, three significant perturbations affected the estuary throughout the 31 month monitoring program: 1) the diversion of wastewater

to the ocean outfall in March 2010, 2) a 6.3 magnitude earthquake on 22 February 2011 and, 3) a 6.3 magnitude earthquake on 13 June 2011.

2.2.2. Field monitoring and sampling protocols

To examine temporal and spatial changes in communities and sediments, 15 0.5m x 0.5m quadrats were positioned randomly along a fixed 30m transect at each site on each sampling occasion. These transects were originally set up prior to the wastewater diversion for sampling habitats along a eutrophication gradient. The position of the transects were not altered after the earthquakes as the aim was to examine overall site changes and effects through time via the continued use of prior transects. A direct comparison of old and new sediments after the earthquakes is covered in *Chapter 3*. In each quadrat, the percentage cover of marine plants (algae and seagrass) and counts of fauna >0.5cm in length occurring in the top 2cm of sediment (hereafter referred to as “surface fauna”) were recorded. Where marine plant cover was ≥2%, plants were collected and processed for biomass in the laboratory. A sediment core (20cm length; 9cm diameter) was extracted adjacent to five randomly selected quadrats at each site for the collection of infauna. Note that “infauna” here also includes any epifauna present within a sediment core. Cores were sieved through a 500µm mesh and retained infauna stored in 70% ethanol and later processed in the laboratory. Surface (<2cm deep) sediment samples were also collected from five randomly selected quadrats at each site. Samples were frozen at -20°C prior to processing for grain size and organic content.

2.2.3. Laboratory procedures

2.2.3.1. Infauna

Infauna were sorted and identified to the lowest practical taxonomic level, which was generally to genus and often to species. Precision at these taxonomic levels has been reported as sufficient for resolving community patterns (Agard et al. 1993, James et al. 1995) and reflecting species-level biodiversity in similar habitats (Gaston 2000, Olsgard et al. 2003). Counts were obtained to determine taxon abundances per sample.

2.2.3.2. Marine plants

Samples of marine plants were washed thoroughly to extract all associated fauna. Fauna were counted and identified to the lowest practical taxonomic level, as above. Marine plant samples were separated into individual taxon and each taxon dried separately (60°C for 3-7d) to obtain the dry biomass.

2.2.3.3. Sediment

Sediment samples were well-mixed and two sub-samples of c. 20g were taken from each sample for analyses. One sample was dried (60°C for 3d) and then ashed (550°C for 5h) to calculate organic content. The organic content was calculated by subtracting the combusted weight from the dry weight and this was expressed as the percentage of sediment dry weight.

The other sample was dried at 60°C for 3d and put through a series of sieves (500µm, 250µm, 125µm, 63µm) to determine the fraction of sediment in each size class (250-500µm (“>250µm”) = medium sand, 125-250µm = fine sand, 63-125µm = very fine sand, <63µm = silt). Most samples were sieved as wet sediment to determine grain size but a small number were sieved after drying. A comparison of techniques was done on 16 samples analysed using both wet and dry sieving methods. Linear regression showed a high level of agreement (R^2 = 0.76 – 0.96) when comparing the outputs using both methods (Fig. 2.1).

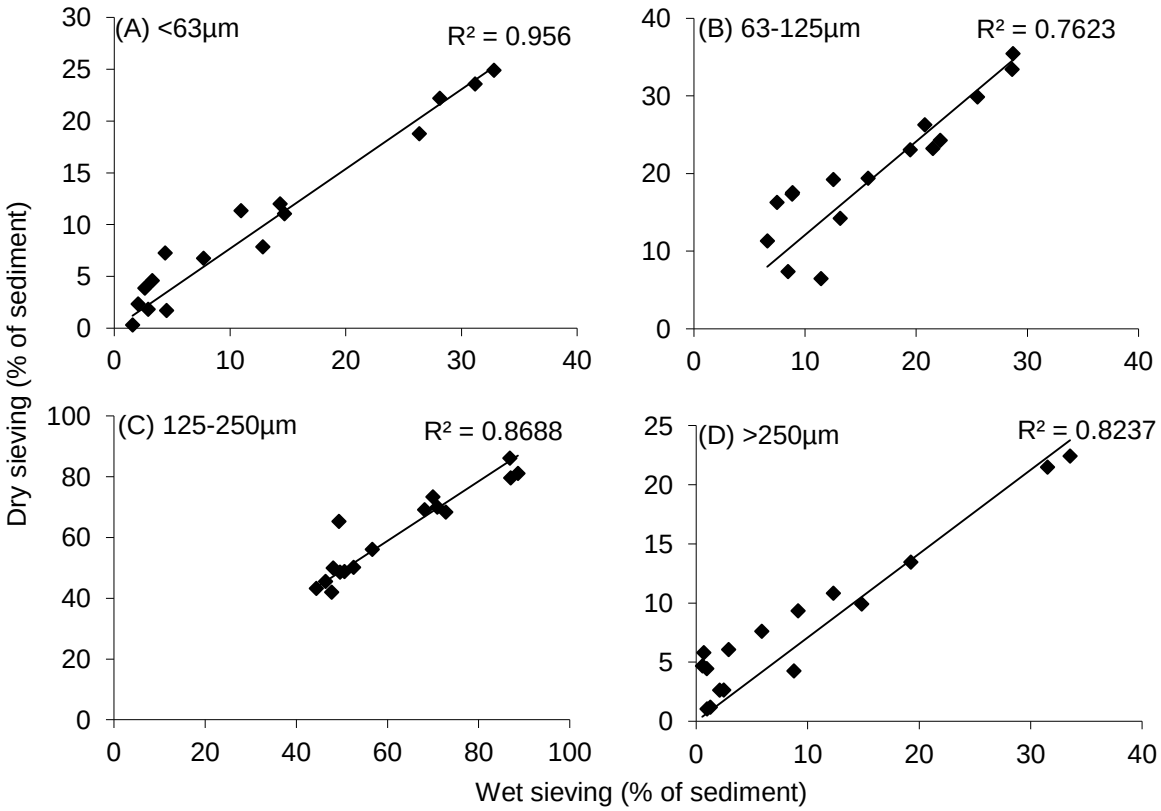

Figure 2.1. Comparison between wet and dry sieving techniques for 16 sediment samples for four grain size classes: <63µm (A), 63-125µm (B), 125-250µm (C), >250µm (D).

2.2.4. Statistical Analyses

The infauna and surface fauna data were each fourth-root transformed and a resemblance matrix constructed using Bray-Curtis measure of similarity. Permutation analysis of variance (PERMANOVA) were performed with the factors site (fixed; 7 levels), sampling period (fixed; 3 levels: pre-diversion, post-diversion/pre-earthquake and post-earthquake) and date nested within sampling period (random). Site was considered a fixed factor as each site represented a point on a eutrophication gradient. SIMPER analyses, to identify the species responsible for spatial and temporal differences, were performed and taxa richness and the number of individuals among sites and dates were plotted using line graphs. Principle Coordinate Ordination (PCO) plots showed patterns of community composition with Spearman's vectors overlaid to indicate the individual taxa influencing these.

General linear models were applied to each of the marine plant taxa (benthic microalgae (BMA), *Gracilaria chilensis*, *Ulva* spp. and *Zostera muelleri*) to examine spatial and temporal differences in percentage cover and biomass. The model used sites (fixed; 7 levels), sampling periods (fixed; 3 levels: pre-diversion, post-

diversion/pre-earthquake and post-earthquake) and dates nested within sampling periods (random). An overall PERMANOVA analysis was run for both the percentage cover and biomass data to examine overall marine plant community composition. Here, data were fourth-root transformed and a resemblance matrix constructed using Bray-Curtis measure of similarity. Factors were site (7 levels; fixed), sampling period (fixed; 3 levels: pre-diversion, post-diversion/pre-earthquake and post-earthquake) and date nested within sampling period (random).

Marine plant samples collected at Humphreys were observed to contained high numbers of associated faunal species. Consequently, samples at this site were processed to examine temporal changes in the community composition of the fauna associated with marine plants. Changes were examined using PERMANOVA, with sampling dates (random) as the single factor. SIMPER analyses were run to show the marine plant associated fauna contributing to 90% of the community at Humphreys across the four sampling dates (December 2009, February 2010, January 2011 and January 2012). Principle Coordinate Ordination plots showed patterns of community composition with Spearman's vectors overlaid to indicate the individual taxa influencing these.

Sediment grain size and organic content data were analysed using univariate general linear models (GLMs) with grain size/organic content as the response variable and site (7 levels; fixed), sampling period (fixed; 3 levels: pre-diversion, post-diversion/pre-earthquake and post-earthquake) and date nested within sampling period (random) as categorical predictor variables. Where necessary, data were log-transformed to fulfil the assumptions of the model and where Cochran's test for homogeneity of variances remained significant following data transformation, p-values were made more conservative by reducing the significance threshold from 0.05 to 0.01 (Underwood 1997). Tukey post-hoc tests were performed to examine directions of significant relationships.

After analysing individual datasets, a DistLM analysis was run to evaluate the predictive effects of marine plant biomass, marine plant percentage cover, sediment organic content and sediment grain size on infaunal and surface faunal community composition. Overall PCO plots were produced to show the marine plant and sediment predictor variables influencing the composition of faunal communities over spatial and temporal scales.

Community analyses were done using PRIMER 6 & PERMANOVA and GLMs were performed using STATISTICA 7.

2.3. Results

2.3.1. Infauna

There were significant effects of site, date(sampling period), site x sampling period and site x date(sampling period) on infaunal community composition (Table 2.1). Infaunal taxa richness was variable through time but did not obviously relate to the diversion or earthquake events (Fig. 2.2A-G). Highest taxa richness occurred at Heron 2 (8.6 - 11.4 taxa per 0.0013m^2) and lowest richness occurred at Humphreys, where <5 taxa per 0.0013m^2 were found on all sampling dates. At Avon and Discharge, taxa richness increased slightly between January 2011 and July 2011 after the February and June 2011 earthquakes.

With the exception of the initial sampling period at Discharge, the average number of individuals of infauna found across all sites and dates was <100 individuals per 0.0013m^2 (Fig. 2.2H-N). The lowest number of individuals occurred at Humphreys. At Avon, Discharge and Heathcote, there was a small increase in the number of individuals between January 2011 and July 2011 after the earthquake. At Heron, there was an increase in the number of individuals between February 2010 and July 2010 (after the diversion) and at Pukeko, the number of infauna individuals decreased between July 2011 and January 2012.

Infaunal community composition at the initial (December 2009) and final (July 2012) sampling dates was almost identical at Avon and similar at the two Heron sites, even though there was considerable variation over time (Fig 2.3B-D). All other sites showed both considerable variation through time and quite different communities by the end sampling date (Fig. 2.3A,E-G).

Table 2.1. PERMANOVA for infauna and surface fauna community composition with two factors: Site (fixed; 7 levels: Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys, Pukeko) and sampling period (3 levels: pre-diversion (December 2009, February 2010), post-diversion/pre-earthquake (July 2010, January 2011) and post-earthquake (July 2011, January 2012, July 2012). Note that Heron 2 and Humphreys were not sampled in July 2010 and July 2011, and Heathcote was not sampled in December 2009. N=5 replicates per site per sampling date.

	Infauna			Surface Fauna		
	DF	**Pseudo-F**	**p**	**DF**	**Pseudo-F**	**p**
Site	6	12.03	**<0.001**	6	27.62	**<0.001**
Sampling period	2	1.32	0.22	2	0.91	0.62
Date(sampling period)	4	4.20	**<0.001**	4	14.24	**<0.001**
Site*sampling period	12	1.88	**0.0013**	12	3.46	**<0.001**
Site*date(sampling period)	17	2.45	**<0.001**	17	7.34	**<0.001**

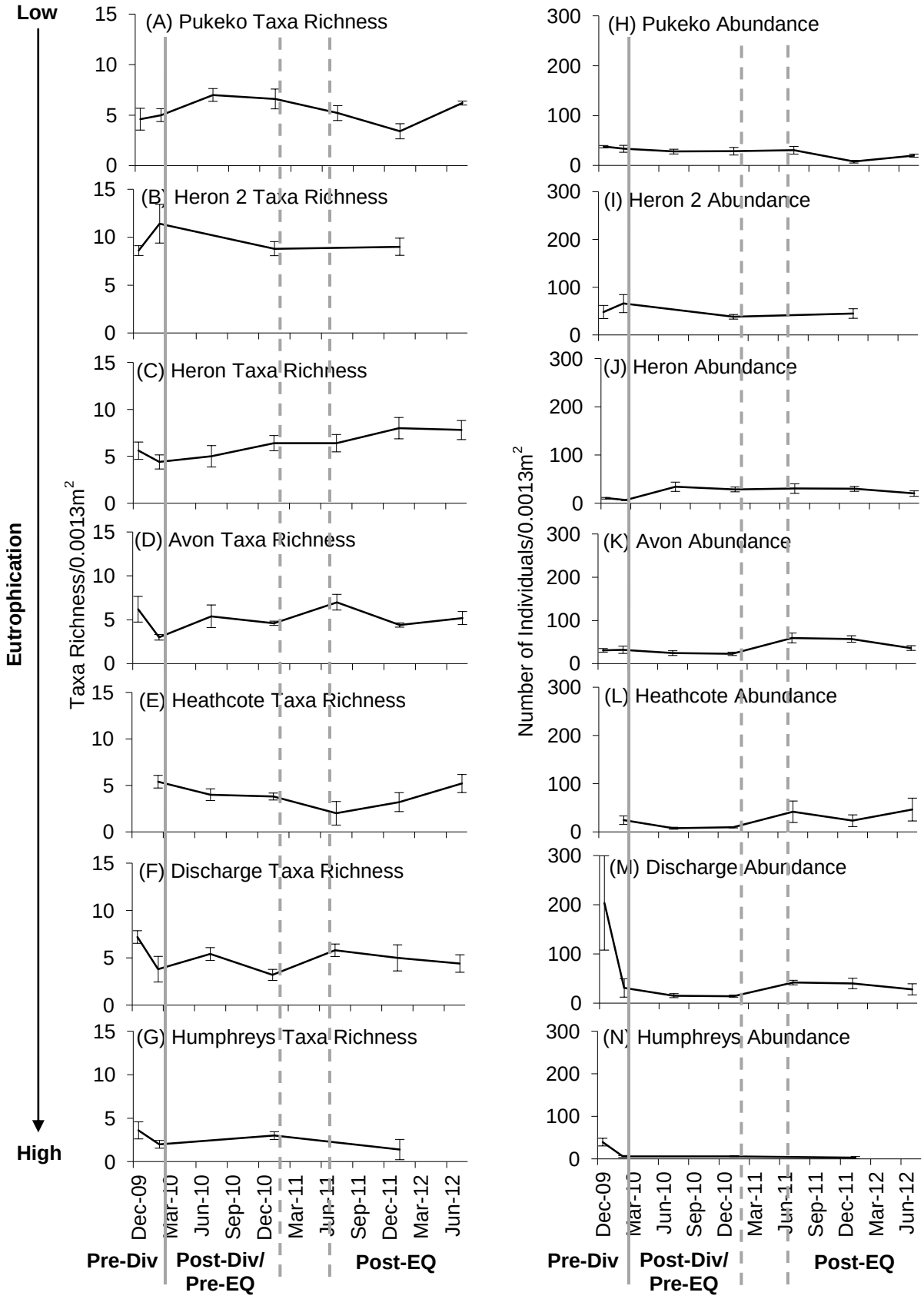

Figure 2.2. Average (±SE) taxa richness of infauna at seven sites (Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys and Pukeko) for sampling dates from December 2009 to July 2012. Solid grey line indicates timing of the diversion (March 2010) and the dashed grey lines indicate the timing of the February 2011 and June 2011 earthquakes. N=5 replicates per site per sampling date.

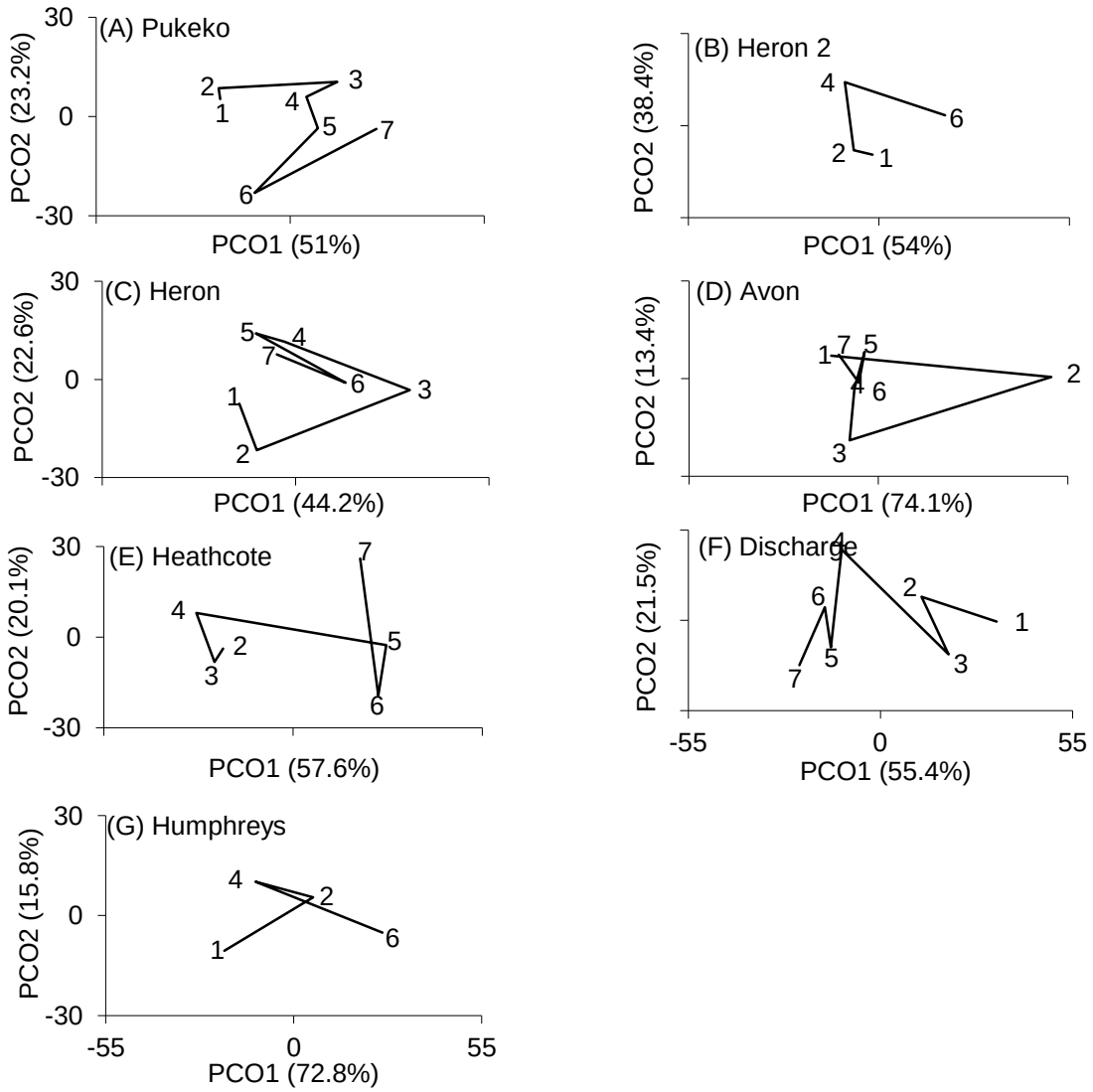

Figure 2.3. PCO plots based on distance to centroid for infauna community composition at each of the seven sites over 5-7 sampling dates. 1=December 2009, 2=February 2010, 3=July 2010, 4=January 2011, 5=July 2011, 6=January 2012, 7=July 2012. PCO percentages are percentage of total variation. N=5 replicates per site per sampling date. Sites are ordered in a eutrophication gradient from low (A) to high (G).

The sites could be separated along a eutrophication gradient but with some overlap based on their infaunal community composition (Fig. 2.4). In particular, there was no overlap in the groupings of the “clean” and river sites. Community composition at the “clean” sites appeared to be largely underpinned by *Austrovenus stutchburyi*, *Macomona liliana*, *Aonoides* sp. and *Aglaophamus macroura* whereas communities at the river sites were more influenced by *Potamopyrgus estuarinus* and *Nicon aestuariensis.* Communities at the eutrophic sites overlapped communities at both the “clean” and river sites and were largely underpinned by *Parcorophium* sp. *and Nicon.*

SIMPER analyses showed a reduction in Capitellidae at Discharge over the three sampling periods but an increase in the contribution of this taxa to the communities at Heathcote and Heron over this time (Table 2.2). The freshwater snail *Potomopyrgus* became less abundant at Avon over the three sampling periods. *Aonoides* sp. were the most abundant taxa at Heron 2 and Pukeko across all sampling periods. In general, dissimilarity indices were high (58.19 - 93.75) among sites over all sampling periods although some sites, particularly Avon and Discharge, became more similar over time. Within-site similarity of infauna communities increased over the three sampling periods at Avon and Discharge whereas Pukeko, and especially Humphreys, showed a clear reduction of within-site similarity over the three sampling periods.

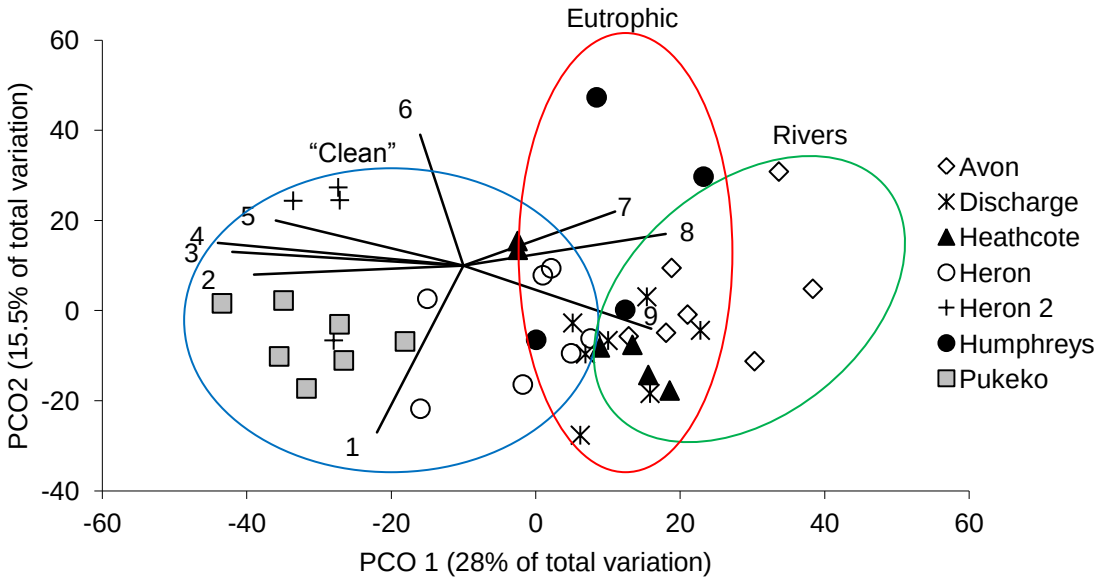

Figure 2.4. PCO plot for infauna based on averages for each sampling date at each site. Each data point represents a sampling date (December 2009, February 2010, June 2010, January 2011, July 2011, January 2012, July 2012 for Avon, Discharge, Heron and Pukeko; February 2010, June 2010, January 2011, July 2011, January 2012, July 2012 for Heathcote; December 2009, February 2010, 2011, January 2012 for Heron 2 and Humphreys). 1=*Scolelpis* sp.; 2=*Austrovenus stutchburyi*; 3=*Macomona liliana*; 4=*Aonoides* sp.; 5=*Aglaophamus macroura*; 6=*Paracalliope* sp.; 7=*Parcorophium* sp.; 8=*Potamopyrgus estuarinus*; 9=*Nicon aestuariensis.* N=5 replicates per site per sampling date. Vectors are shown for Spearman's correlations >0.7. Circles show site groupings along a eutrophication gradient. "Clean" sites (blue circle) = Heron, Heron 2 and Pukeko, "eutrophic" sites (red circle) = Humphreys and Discharge, and "rivers" (green circle) = Avon and Heathcote.

Table 2.2. SIMPER analysis showing infauna taxa contributing to 90% of community at seven sites (Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys, Pukeko) during three sampling periods (pre-diversion, post-diversion/pre-earthquake, post-earthquake). N=5 replicates per site per sampling date.

Gradient	Site	Pre-Diversion			Post-Diversion/Pre-EQ			Post-EQ		
		Taxa	Av.Abund	Contrib%	Taxa	Av.Abund	Contrib%	Taxa	Av.Abund	Contrib%
"clean"	Pukeko	*Aonides* sp.	2.3	57.03	*Aonides* sp.	1.71	31.28	*Aonides* sp.	1.28	31.7
"clean"	Pukeko	*Austrovenus stutchburyi*	1.01	17.45	*Scolepis*	1.5	26.57	*Austrovenus stutchburyi*	0.84	24.39
"clean"	Pukeko	*Macomona liliana*	0.93	16.17	*Austrovenus stutchburyi*	1.37	25.79	*Scolepis*	0.98	18.19
"clean"	Pukeko				*Macomona liliana*	0.58	4.55	*Arthritica* sp.	0.63	14.86
"clean"	Pukeko				Capitellidae	0.61	4.38	Capitellidae	0.29	2.15
"clean"	Heron 2	*Aonides* sp.	2.08	22.77	*Aonides* sp.	1.7	19.63	*Aonides* sp.	2.06	31.05
"clean"	Heron 2	*Haploscoloplos cylindrifer*	1.52	18.1	*Notoacmea helmsi*	1.55	18.15	Capitellidae	1.29	20.59
"clean"	Heron 2	*Austrovenus stutchburyi*	1.11	14.5	*Haploscoloplos cylindrifer*	1.5	18.01	*Haploscoloplos cylindrifer*	1.14	13.66
"clean"	Heron 2	*Microlenchus tenebrosus*	1.2	10.45	*Microlenchus tenebrosus*	1.36	15.73	*Macomona liliana*	0.9	11.38
"clean"	Heron 2	*Macomona liliana*	0.92	8.49	*Paracalliope*	1.08	9.38	*Austrovenus stutchburyi*	0.86	9.9
"clean"	Heron 2	*Arthritica* sp.	0.9	8.09	Capitellidae	0.97	8.15	*Notoacmea helmsi*	0.75	4.3
"clean"	Heron 2	*Halicarnus* sp.	0.66	4.36	*Macomona liliana*	0.64	4.42			
"clean"	Heron 2	Capitellidae	0.63	3.97						
"clean"	Heron	*Scolecolepides benhami*	1.07	43.98	Capitellidae	1.38	29.03	*Scolecolepides benhami*	1.24	21.68
"clean"	Heron	*Haploscoloplos cylindrifer*	0.74	15.95	*Scolecolepides benhami*	1.3	27.55	*Haploscoloplos cylindrifer*	1.08	20.81
"clean"	Heron	*Amphibola crenata*	0.72	14.55	*Nicon aestuariensis*	0.74	12.64	*Scolepis*	0.87	11.69
"clean"	Heron	*Sabelidae*	0.62	14.04	*Arthritica* sp.	0.69	9.86	Capitellidae	0.84	9.19
"clean"	Heron	*Scolepis*	0.4	5.66	*Haploscoloplos cylindrifer*	0.58	6.51	*Arthritica* sp.	0.75	8.17
"clean"	Heron				*Sabelidae*	0.45	4.51	*Amphibola crenata*	0.63	6.7
"clean"	Heron							*Nicon aestuariensis*	0.57	6.37
"clean"	Heron							*Sabelidae*	0.56	4.86
"clean"	Heron							*Boccarda polybranchia*	0.46	3.47
River	Avon	*Potamopyrgus estuarinus*	1.44	47.27	*Arthritica* sp.	1.51	33.69	*Arthritica* sp.	2.31	38.69
River	Avon	*Arthritica* sp.	1.14	22.38	*Scolecolepides benhami*	1.35	32.74	*Nicon aestuariensis*	1.48	24.63
River	Avon	*Nicon aestuariensis*	0.66	10.28	*Nicon aestuariensis*	1.1	21.44	*Scolecolepides benhami*	1.26	17.04
River	Avon	*Scolecolepides benhami*	0.49	5.13	*Potamopyrgus estuarinus*	0.72	6.76	*Potamopyrgus estuarinus*	1.27	15.08
River	Avon	*Paracalliope*	0.33	4.44						
River	Avon	*Paracorophium*	0.33	2.69						
River	Heathcote	*Austrovenus stutchburyi*	1.1	37.92	*Austrovenus stutchburyi*	1.23	47.77	Capitellidae	1.26	42.47
River	Heathcote	*Arthritica* sp.	0.96	22.2	*Arthritica* sp.	1	27.18	*Scolecolepides benhami*	0.63	19.9
River	Heathcote	*Scolecolepides benhami*	0.66	14.79	*Haploscoloplos cylindrifer*	0.74	14.7	*Scolepis*	0.7	13.07
River	Heathcote	*Macrophthalmus hirtipes*	0.48	6.05	*Nicon aestuariensis*	0.54	8.54	*Nicon aestuariensis*	0.53	10.18
River	Heathcote	*Aglaophamus macroura*	0.4	5.58				*Amphibola crenata*	0.52	9.25
River	Heathcote	*Haploscoloplos cylindrifer*	0.51	4.97						
Eutrophic	Discharge	Capitellidae	1.53	26.97	*Scolecolepides benhami*	1.39	56.77	*Arthritica* sp.	1.82	35.71
Eutrophic	Discharge	*Scolecolepides benhami*	1.35	26.6	Capitellidae	0.75	11.54	*Scolecolepides benhami*	1.59	25.48
Eutrophic	Discharge	*Boccarda polybranchia*	1.93	23.38	*Arthritica* sp.	0.54	10.9	*Nicon aestuariensis*	1.19	24.69
Eutrophic	Discharge	*Mactra ovata*	0.84	9.6	*Nicon aestuariensis*	0.42	5.95	*Macrophthalmus hirtipes*	0.68	8.38
Eutrophic	Discharge	*Nicon aestuariensis*	0.44	3.87	*Austrovenus stutchburyi*	0.4	5.47			
Eutrophic	Humphreys	Capitellidae	1.69	84.28	Capitellidae	1.25	72.55	*Capitellidae*	0.53	100
Eutrophic	Humphreys	*Arthritica* sp.	0.47	8.49	*Paracalliope*	0.64	18.3			

2.3.2. Surface fauna

There were significant effects of site, date(sampling period), site x sampling period and site x date(sampling period) on the community composition of surface fauna (Table 2.1). Prior to the diversion, taxa richness was highest at the two cleanest sites, Pukeko and Heron 2 (Fig. 2.5A-G). Heron 2 showed the highest taxa richness across all sites with an average of 6.8-9.7 taxa per 0.25m^2 recorded over the sampling dates. Humphreys, the most eutrophic site, had the lowest taxa richness with an average richness of <1 taxon per 0.25m^2 on all sampling dates. After the diversion and before the February 2011 earthquake, there were no significant changes in taxa richness at any of the sites. But, the surface faunal communities at the river sites appeared to have been affected by the earthquakes with clear reductions in taxa richness at Avon and Heathcote occurring after the events. At Heathcote, taxa richness after the earthquakes decreased from an average of 3 to 0.33 taxa. A very small amount of recovery, to pre-earthquake levels, was seen at this site by July 2012. At Heron, taxa richness was variable between December 2009 and July 2011 but there was a clear increase between July 2011 and July 2012 after the earthquakes.

Similar to the taxa richness of surface fauna, patterns seen for the number of individuals were also generally related to the site eutrophication gradient (Figs. 2.5H-N). The number of surface faunal individuals was highest at Heron 2, where values peaked in February 2010 at 420 individuals per 0.25m^2. Values were low at Discharge but lowest at Humphreys, where an average of <2 individuals per 0.25m^2 were found on all sampling dates. The number of individuals at Pukeko increased after the diversion but decreased dramatically at Heron. The number of individuals at the remaining sites did not change significantly after the diversion and before the earthquakes. The cleanest site, Pukeko, showed no discernible effects of the earthquakes. Similarly, surface faunal communities at Discharge and Humphreys were generally unresponsive but at these sites, this was probably due to them working from a very low base as there were very low numbers of individuals at these eutrophic sites. The river sites, Avon and Heathcote, showed a clear reduction in the number of individuals after the earthquakes. The number of individuals at Heathcote reduced from 56.7 to 1.3 individuals per 0.25m^2 after the February and June 2011 events. There was little evidence of recovery to pre-earthquake levels over the

remaining sampling dates at this site. At Avon, however, recovery to pre-earthquakes levels had occurred by January 2012.

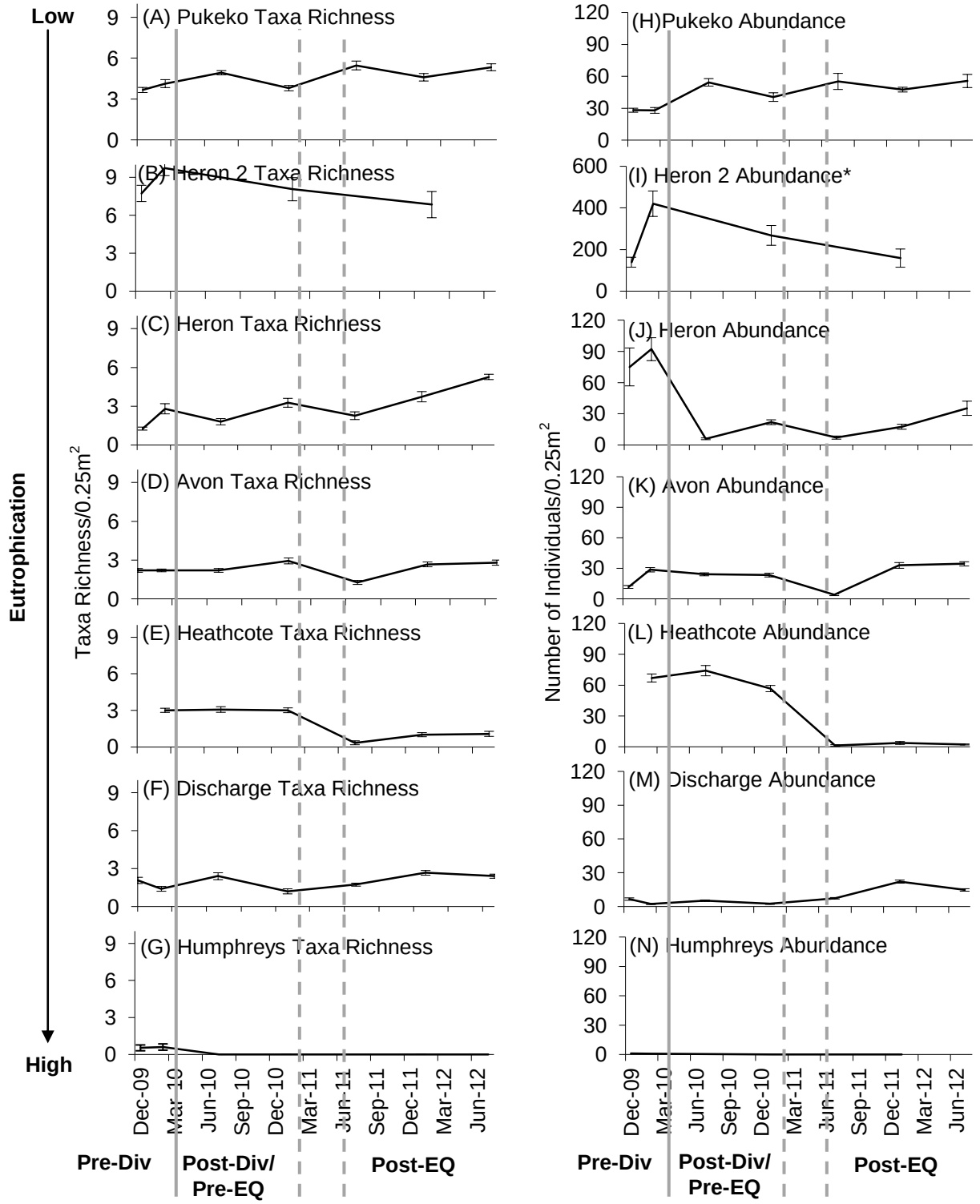

Figure 2.5. Average (±SE) diversity of surface invertebrates (>0.5mm; top 2 cm of sediment) at seven sites (Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys and Pukeko) for sampling dates from December 2009 to July 2012. Solid grey line indicates timing of the diversion (March 2010) and the dashed grey lines indicate the timing of the February 2011 and June 2011 earthquakes. N=15 replicates per site per sampling date. *Note the different y-axis scale for (I).

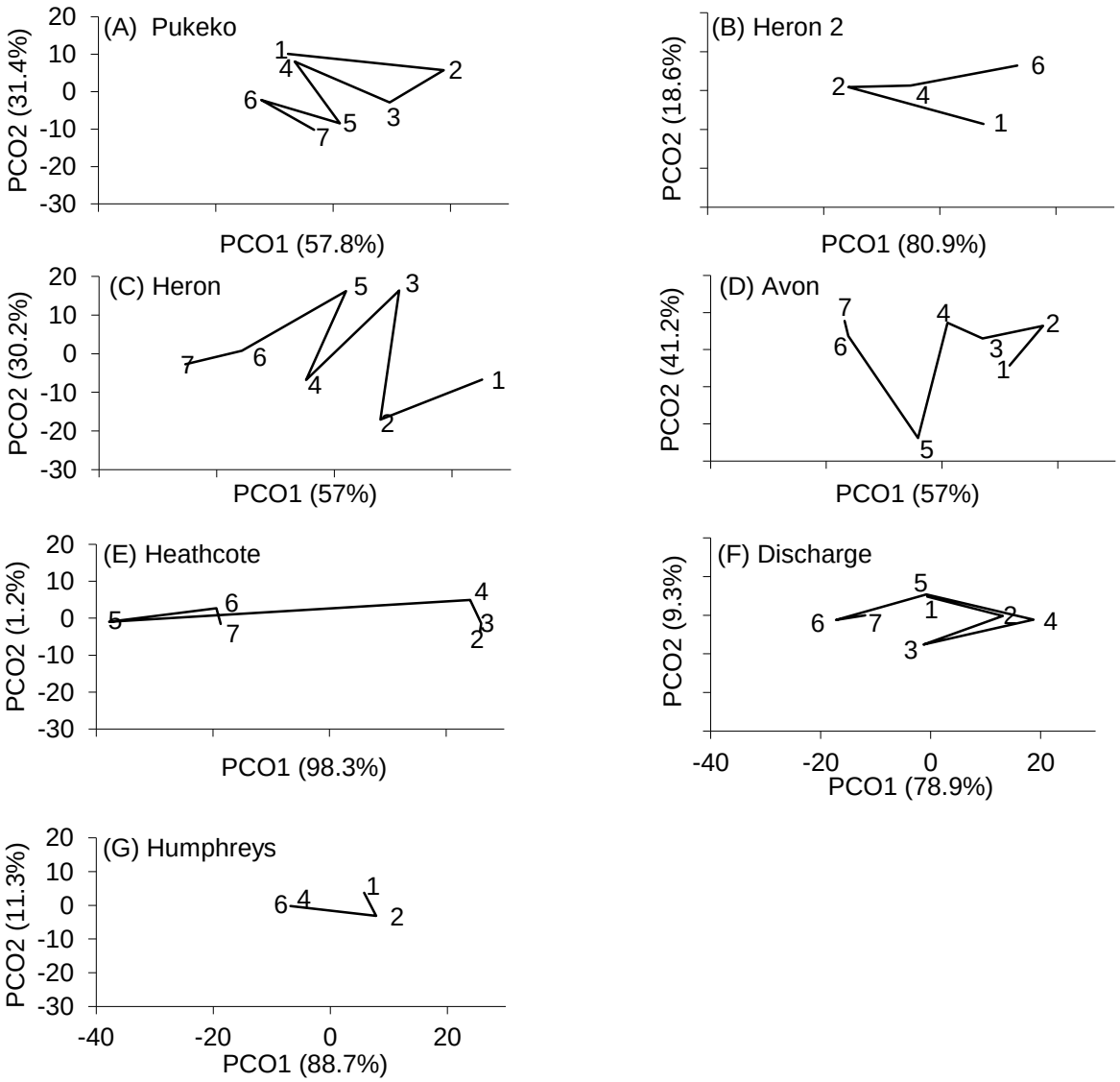

Figure 2.6. PCO plots based on distance to centroid for surface fauna community composition at each of the seven sites over 5-7 sampling dates. 1=December 2009, 2=February 2010, 3=July 2010, 4=January 2011, 5=July 2011, 6=January 2012, 7=July 2012. 1&2=pre-diversion, 3&4=post-diversion/pre-earthquake, 5-7=post earthquake. PCO percentages are percentage of total variation. N=15 replicates per site per sampling date. Sites are ordered in a eutrophication gradient from low (A) to high (G).

The surface faunal communities of all sites changed considerably through time and none converged with their initial state (Fig. 2.6A-G). In most cases, the gradient changes were seen between periods 4 (before) and 5-7 (after) the earthquakes hit. Overall, the river sites, especially Heathcote, showed the largest variation through time and the most polluted sites (Discharge and Humphreys) the least because of the depauperate community.

When plotted together, there was some grouping of surface faunal communities based on site and eutrophication status but with considerable overlap in some cases (Fig. 2.7). The tightest groupings were seen for the cleaner sites of

Pukeko and Heron 2. In particular, Heron 2 formed a distinct cluster, separated from any other site. Vectors indicated that the distinction of this site was strongly influenced by the abundance of *Austrovenus, Cominella, Diloma*, *Notoacmea* and *Microlenchus.* Discharge, Heathcote, Avon and Heron all showed considerable overlap and were more variable temporally. The eutrophic sites, Humphreys and Discharge, had different communities but this was due to very few species at these sites, particularly at Humphreys.

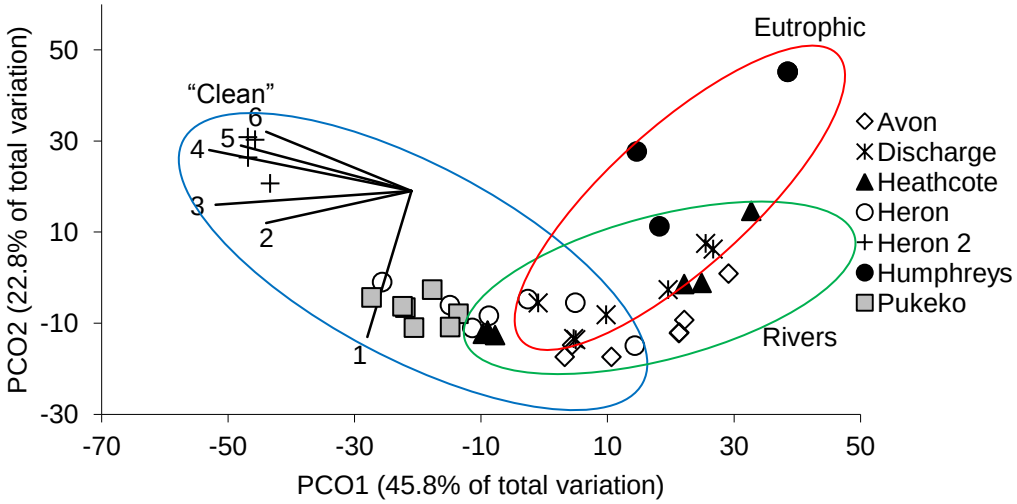

Figure 2.7. PCO plot for surface fauna based on averages for each sampling date at each site. Each data point represents a sampling date (December 2009, February 2010, June 2010, January 2011, July 2011, January 2012, July 2012 for Avon, Discharge, Heron and Pukeko; February 2010, June 2010, January 2011, July 2011, January 2012, July 2012 for Heathcote; December 2009, February 2010, January 2011, January 2012 for Heron 2 and Humphreys). 1=*Amphibola crenata*, 2=*Austrovenus stutchburyi*, 3=*Cominella glandiformis*, 4=*Diloma subrostrata*, 5=*Notoacmea helmsi*, 6=*Microlenchus tenebrosus*. Vectors are shown for Spearman's correlations >0.7. N=15 replicates per site per sampling date. "Clean" sites (blue circle) = Heron, Heron 2 and Pukeko, "eutrophic" sites (red circle) = Humphreys and Discharge, and "rivers" (green circle) = Avon and Heathcote.

SIMPER analyses showed that, in nearly all cases, *Austrovenus* contributed to 90% of the community at all sites across all sampling periods (Table 2.3). At Avon, there was a reduction in the contribution of *Austrohelice* during the post-earthquake period but at Discharge, *Amphibola* and *Austrovenus* were the only two species contributing to 90% of the community across all sampling periods. At Heron, there was an increase from one taxa to five taxa, contributing to 90% of the community between the first and final sampling periods. The greatest number of taxa (8) contributing to 90% of the community occurred at Heron 2 during the first two sampling periods.

Table 2.3. SIMPER analysis showing surface fauna taxa contributing to 90% of community at seven sites (Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys, Pukeko) during three sampling periods (pre-diversion, post-diversion/pre-earthquake, post-earthquake). N=15 replicates per site per sampling date.

Gradient	Site	Pre-Diversion taxa	Av.Abund	Contrib%	Post-Div/Pre-EQ taxa	Av.Abund	Contrib%	Post-EQ taxa	Av.Abund	Contrib%
"Clean"	Pukeko	*Amphibola crenata*	1.78	42.05	*Amphibola crenata*	1.91	32.18	*Austrovenus stutchburyi*	2.14	32.49
"Clean"		*Diloma subrostrata*	1.39	28.61	*Austrovenus stutchburyi*	1.89	30.52	*Amphibola crenata*	1.75	26.7
"Clean"		*Austrovenus stutchburyi*	1.21	18.54	*Diloma subrostrata*	1.52	22.96	*Diloma subrostrata*	1.38	16.8
"Clean"		*Notoacmea* sp.	0.66	6.47	*Notoacmea* sp.	1.13	8.77	*Notoacmea* sp.	1.1	9.86
"Clean"								*Eliminus*	1.06	9.13
"Clean"	Heron 2	*Microlenchus tenebrosus*	3.09	22.42	*Microlenchus tenebrousa*	2.82	18.55	*Austrovenus stutchburyi*	2.16	36.21
"Clean"		*Austrovenus stutchburyi*	2.11	18.37	*Diloma subrostrata*	1.85	17.72	*Diloma subrostrata*	1.65	31.79
"Clean"		*Diloma subrostrata*	1.98	14.68	*Austrovenus stutchburyi*	1.98	17.68	*Microlenchus tenebrousa*	1.63	7.39
"Clean"		*Notoacmea* sp.	1.93	12.91	*Notoacmea* sp.	1.91	11.61	*Cominella glandiformis*	0.84	6.68
"Clean"		*Macrophthalmus hirtipes*	1.45	9.25	*Macrophthalmus hirtipes*	1.4	6.95	*Notoacmea* sp.	1.14	5.78
"Clean"		*Hemigrapsus crenulatus*	1.05	6.92	*Macomona*	1.44	6.63	*Macomona*	0.69	2.71
"Clean"		*Cominella glandiformis*	0.88	4.58	*Halicarcinus*	1.2	6.53			
"Clean"		*Halicarcinus*	1.03	4.01	*Hemigrapsus crenulatus*	1.02	6.29			
"Clean"	Heron	*Amphibola crenata*	2.89	95.52	*Amphibola crenata*	1.65	79.97	*Amphibola crenata*	1.49	47.36
"Clean"					*Diloma subrostrata*	0.52	7.9	*Austrovenus stutchburyi*	0.87	17.17
"Clean"					*Cominella glandiformis*	0.49	6.67	*Cominella glandiformis*	0.8	14.78
"Clean"								*Diloma subrostrata*	0.79	10.2
"Clean"								*Microlenchus tenebrousa*	0.73	7.72
River	Avon	*Amphibola crenata*	1.91	62.95	*Amphibola crenata*	2.09	66.44	*Amphibola crenata*	1.89	67.91
River		*Austrohelice crassa*	1.25	34.29	*Austrohelice crassa*	0.92	19.39	*Austrovenus stutchburyi*	1.13	29.61
River					*Austrovenus stutchburyi*	0.81	13.85			
River	Heathcote	*Austrovenus stutchburyi*	2.66	52.58	*Austrovenus stutchburyi*	2.66	56.05	*Austrovenus stutchburyi*	0.45	55.75
River		*Amphibola crenata*	1.94	38.08	*Amphibola crenata*	1.82	37.33	*Amphibola crenata*	0.46	44.05
Eutrophic	Discharge	*Amphibola crenata*	1.08	74.88	*Amphibola crenata*	0.91	59.44	*Amphibola crenata*	1.78	63.88
Eutrophic		*Austrovenus stutchburyi*	0.63	22.05	*Austrovenus stutchburyi*	0.74	38.8	*Austrovenus stutchburyi*	1.16	34.7
Eutrophic	Humphreys	*Austrovenus stutchburyi*	0.35	93.97						

Crab holes were found at Avon, Discharge, Heathcote and Heron and were generally absent or rare at Heron 2 and Pukeko, the two cleanest sites, and at Humphreys, the most eutrophic site (Fig. 2.8A-G). At sites where they were initially abundant (the two river sites), the number of crab holes (and predicted number of crabs – see Fig. 2.9) decreased after the diversion. The earthquakes did not appear to impact the abundance of crabs at Avon but at Heathcote there may have been a delayed response, with low crab numbers occurring in January and July 2012. At Discharge, one of the most eutrophic sites, the number of crab holes increased after the earthquakes, peaking in July 2011 at 15.3 crab holes per 0.25m^2.

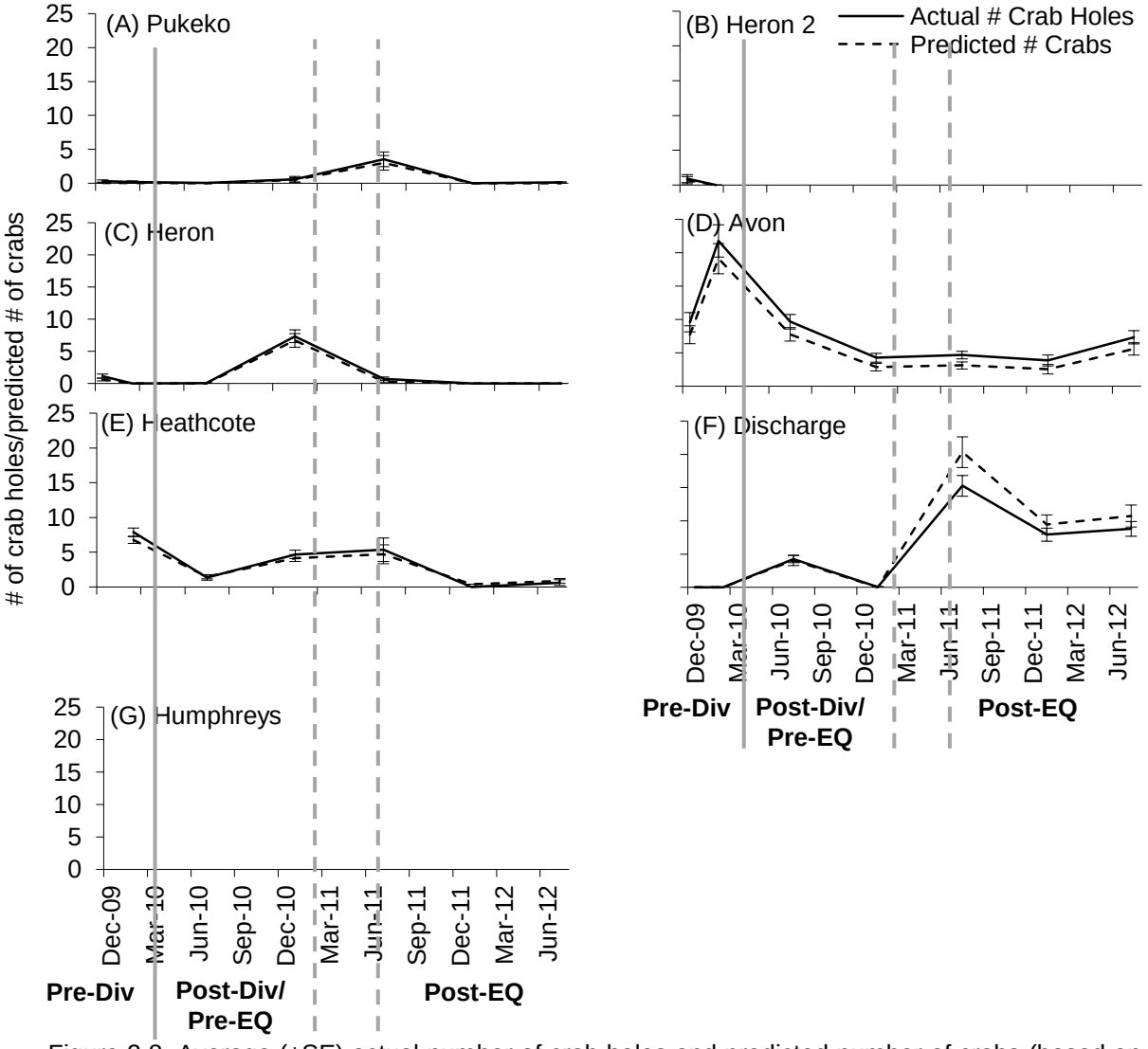

Figure 2.8. Average (±SE) actual number of crab holes and predicted number of crabs (based on regression equations in Fig. 2.9) for each of the seven sites (Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys and Pukeko) for sampling dates between December 2009 and July 2012. Solid grey line indicates timing of the diversion (March 2010) and the dashed grey lines show the timing of the February 2011 and June 2011 earthquakes. N=15 replicates per site per sampling date. Sites are ordered in a eutrophication gradient from low (A) to high (G).

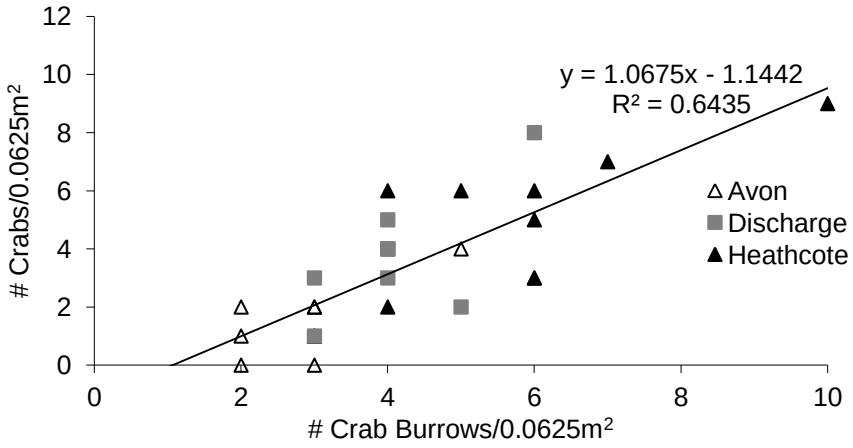

Figure 2.9. Relationship between the number of crab burrows and the number of crabs at three sites (Avon, Discharge and Heathcote) on one sampling occasion. The regression equation and R^2 value are shown on the graph. Site-specific values are: Heathcote: y=0.8077x+0.3761 R^2=0.4288; Avon=0.9355x-1.2581 R^2=0.4933; Discharge: y=1.4839x-2.3226 R^2=0.4807.

2.3.3. Marine plants

Using percentage cover as a metric, the overall community of marine plants differed significantly among sites ($F_{6,17}$=10.59 p<0.001), sampling periods ($F_{2,17}$=4.83 p=0.011), date(sampling period) ($F_{4,17}$=2.48 p=0.015) and site x sampling period ($F_{12,17}$=2.16 p=0.016). Where macroalgae and seagrass were abundant initially, they declined significantly after the diversion and continued declining after the earthquakes (Fig. 2.10). The response of BMA was more variable, however, increasing greatly at two sites but not at the others.

Percentage cover of BMA differed significantly among sites and sampling periods, and all interaction effects were significant (Table 2.4A). Benthic microalgae were absent or rare at Avon, Discharge and Heron 2 across all sampling dates (Fig. 2.10) indicating that the abundance of BMA was not directly related to the eutrophication gradient of sites. Prior to the earthquakes, BMA was absent at Heathcote but it was the only marine plant taxa present at this site after the earthquakes. Benthic microalgae were absent at Humphreys until January 2012 where over 50% of the sampling area was covered with this taxa. This was probably due to the disappearance of macroalgae at this eutrophic site providing opportunity for BMA to flourish in the high-nutrient sedimentary environment. The percentage cover of BMA at Heron was variable temporally, peaking in July 2010 at 28.4%.

There were significant effects of site, site x sampling period and site x date(sampling period) on the percentage cover of *Gracilaria* (Table 2.4B). This

species dominated the marine plant community at Humphreys but declined after the diversion and then disappeared after the earthquakes (Fig. 2.10), most likely because of the uplifting of this site and the change in tidal elevation. *Gracilaria* did not occur at any other site expect for Heathcote in July 2010 where an average of 23.6% of the sampled area was covered with this species.

The percentage cover of *Ulva* differed significantly among sites and the site x date(sampling period) interaction effect was significant (Table 2.4C). *Ulva* occurred at sites representing very different points on the eutrophication gradient (Heron and Heron 2 (“clean”), Heathcote (river) and Humphreys (eutrophic)) prior to the diversion. But after the diversion, *Ulva* largely disappeared from all sites and remained absent or at a low abundance for the remaining sampling periods (Fig. 2.10).

Zostera cover differed significantly among sites and the site x sampling period interaction effect was significant (Table 2.4D). It was absent or rare at most sites. However, at the one site where it was abundant (Heron 2), it declined slightly after the diversion and greatly after the earthquakes (Fig. 2.10), mostly because of burial by liquefied sediments.

Table 2.4. General linear model analysis showing differences in the percentage cover and biomass of benthic microalgae (BMA), *Gracilaria chilensis* (B), *Ulva* spp. (C) and *Zostera muelleri* (D) across sites (fixed; 7 levels: Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys, Pukeko), sampling periods (fixed; 3 levels: pre-diversion (December 2009, February 2010), post-diversion/pre-earthquake (July 2010, January 2011), post-earthquake (July 2011, January 2012, July 2012)) and dates nested within sampling periods. Note that Heron 2 and Humphreys were not sampled in July 2010 and July 2011, and Heathcote was not sampled in December 2009. For percentage cover, N=15 samples per site per sampling date and for biomass, N=7-15 replicates per site per sampling date. *Cochran's C still significant following log transformation so p-value reduced to 0.01.

(A) BMA

	% Cover		
	DF	**F**	**p**
Site	6	4.61	**0.0059**
Sampling period	2	9.61	**0.035**
Date(sampling period)	4	1.33	0.30
Site*sampling period	12	4.72	**0.0020**
Site*date(sampling period)	17	14.86	**<0.001**

(B) *Gracilaria*

	% Cover			Biomass		
	DF	**F**	**p**	**DF**	**F**	**p**
Site	6	38.92	**<0.001**	1	370.11	**<0.001**
Sampling period	2	16.71	0.016*	16	0.17	1
Date(sampling period)	4	0.93	0.47	47	3.32	**<0.001**
Site*sampling period	12	9.30	**<0.001**	22	0.49	0.96
Site*date(sampling period)	17	18.41	**<0.001**	38	74.99	**<0.001**

(C) *Ulva*

	% Cover			Biomass		
	DF	**F**	**p**	**DF**	**F**	**p**
Site	6	8.33	**<0.001**	1	0.00085	0.98
Sampling period	2	2.94	0.17	16	0.46	0.95
Date(sampling period)	4	4.33	0.013*	47	4.00	**<0.001**
Site*sampling period	12	1.58	0.19	22	1.13	0.36
Site*date(sampling period)	17	11.93	**<0.001**	38	19.48	**<0.001**

(D) *Zostera*

	% Cover			Biomass		
	DF	**F**	**p**	**DF**	**F**	**p**
Site	**6**	312.07	**<0.001**	1	413.76	**<0.001**
Sampling period	**2**	8.28	0.043*	16	0.53	0.92
Date(sampling period)	**4**	1.52	0.24	47	3.39	**<0.001**
Site*sampling period	**12**	13.43	**<0.001**	22	0.96	0.53
Site*date(sampling period)	**17**	1.07	0.383	38	18832.82	**<0.001**

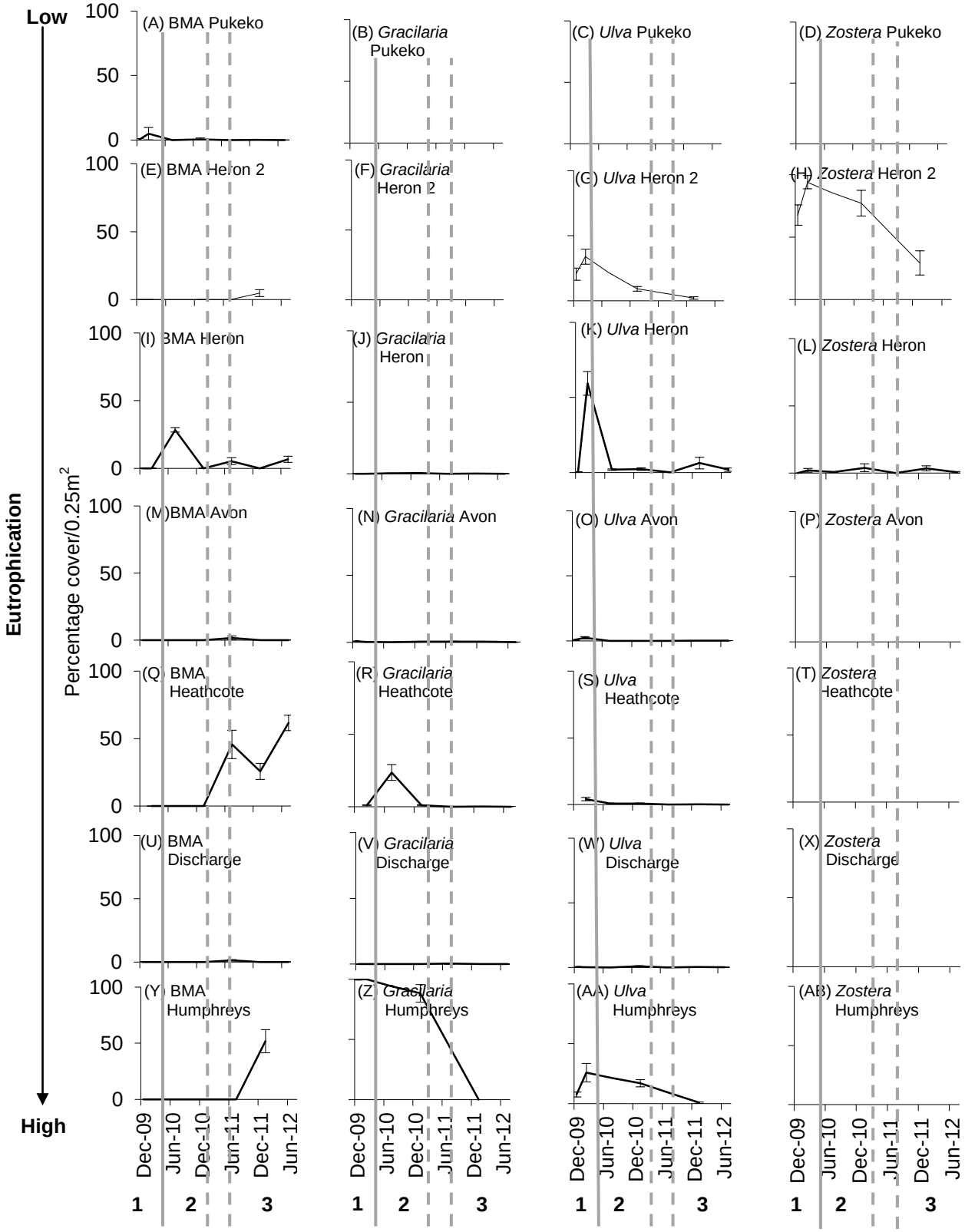

Figure 2.10. Average (±SE) percentage cover of marine plants at seven sites (Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys and Pukeko) over sampling dates from December 2009 to July 2012. Solid grey line indicates timing of the diversion (March 2010) and the dashed grey lines show the timing of the February 2011 and June 2011 earthquakes. 1=pre-diversion, 2=post-diversion/pre-earthquake, 3=post-earthquake. N=15 replicates per site per sampling date. Sites are ordered in a eutrophication gradient from low (A-D) to high (Y-AB).

Scatterplots of percentage cover versus biomass for marine plant data showed strong exponential relationships for *Gracilaria* ($y=e^{0.0461x}$ $R^2=0.8977$) and *Zostera* ($y=e^{0.0411x}$ $R^2=0.7378$). A slightly weaker relationship was found for *Ulva* ($y=e^{0.0468x}$ $R^2=0.5208$) (Fig. 2.11). Marine plant biomass patterns generally tracked that of percentage cover (with the exception of BMA which was not measured for biomass) and the same factors were significant (site: pseudo-$F_{6,17}=15.40$, $p<0.001$; sampling period: pseudo-$F_{2,17}=4.93$, $p=0.018$; site x sampling period: pseudo-$F_{12,17}=2.74$ $p=0.0065$).

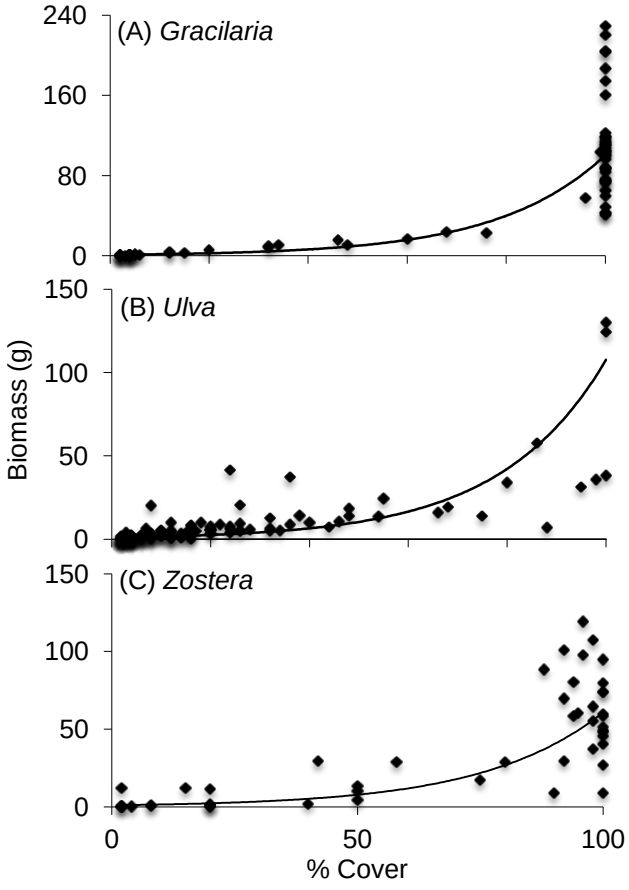

Figure 2.11. Relationship between percentage cover and biomass for *Gracilaria chilensis* (A), *Ulva* spp. (B) and *Zostera muelleri* (C) with fitted exponential curve.

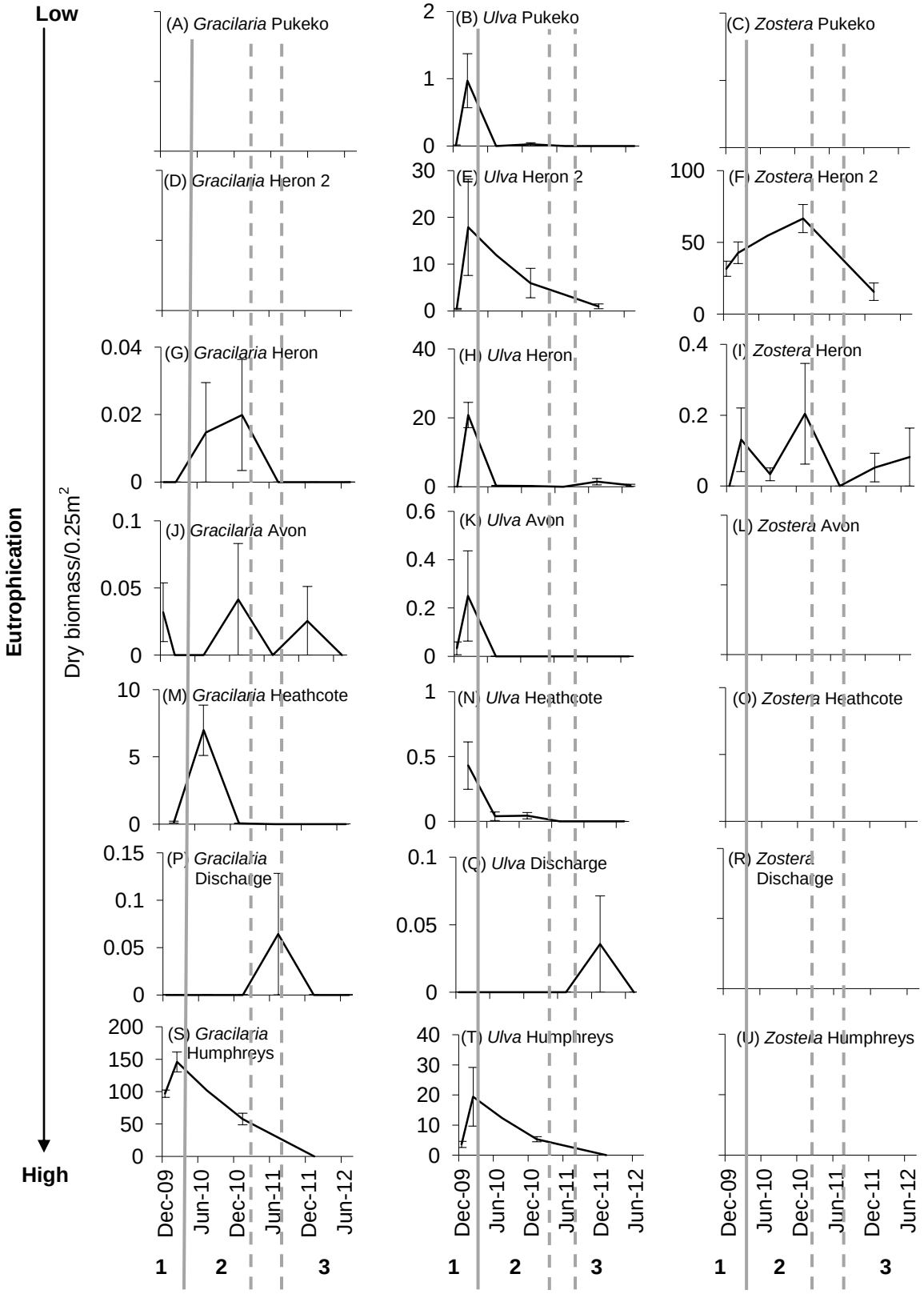

Figure 2.12. Average (±SE) dry biomass of marine plants at seven sites (Avon, Discharge, Heathcote, Heron 1, Heron 2, Humphreys and Pukeko) over sampling dates from December 2009 to July 2012. Solid grey line indicates timing of the diversion (March 2010) and the dashed grey lines show the timing of the February 2011 and June 2011 earthquakes. 1=pre-diversion, 2=post-diversion/pre-earthquake, 3=post-earthquake. N=7-15 replicates per site per sampling date.

There were significant effects of site, date(sampling period) and site x date(sampling period) on the biomass of *Gracilaria* (Table 2.4B). *Gracilaria* was absent or rare at all sites except Humphreys where its biomass decreased after the diversion and continued to decrease after the earthquakes until it disappeared from this site (Fig. 2.12).

There were significant effects of date(sampling period) and site x date(sampling period) on the biomass of *Ulva* (Table 2.4C), with the biomass of this species peaking prior to the diversion at all sites except Discharge (Fig. 2.12). Highest biomass of this species occurred at the most eutrophic site (Humphreys), and two of the cleaner sites, Heron and Heron 2.

The biomass of *Zostera* differed significantly among sites, date(sampling period) and the interaction effect of site x date(sampling period) was significant (Table 2.4D). Biomass of *Zostera* was low or zero at all sites except Heron 2 where it peaked in January 2011 (post-diversion/pre-earthquake) at 66.6g dry weight per $0.25m^2$ (Fig. 2.12).

PCO plots showed a general separation of sites based on their marine plant communities but with considerable overlap among the “clean”, eutrophic and river sites (Fig. 2.13). For both percentage cover and biomass datasets, the distinction of the marine plant community at Heron 2 was underpinned by the abundance of *Zostera* (and to a lesser degree *Ulva*), and at Humphreys (excluding the final sampling date) by the abundance of *Gracilaria* (and to a lesser degree *Ulva*). The marine plant communities at the remaining sites did not obviously appear to be influenced by changes in any particular species.

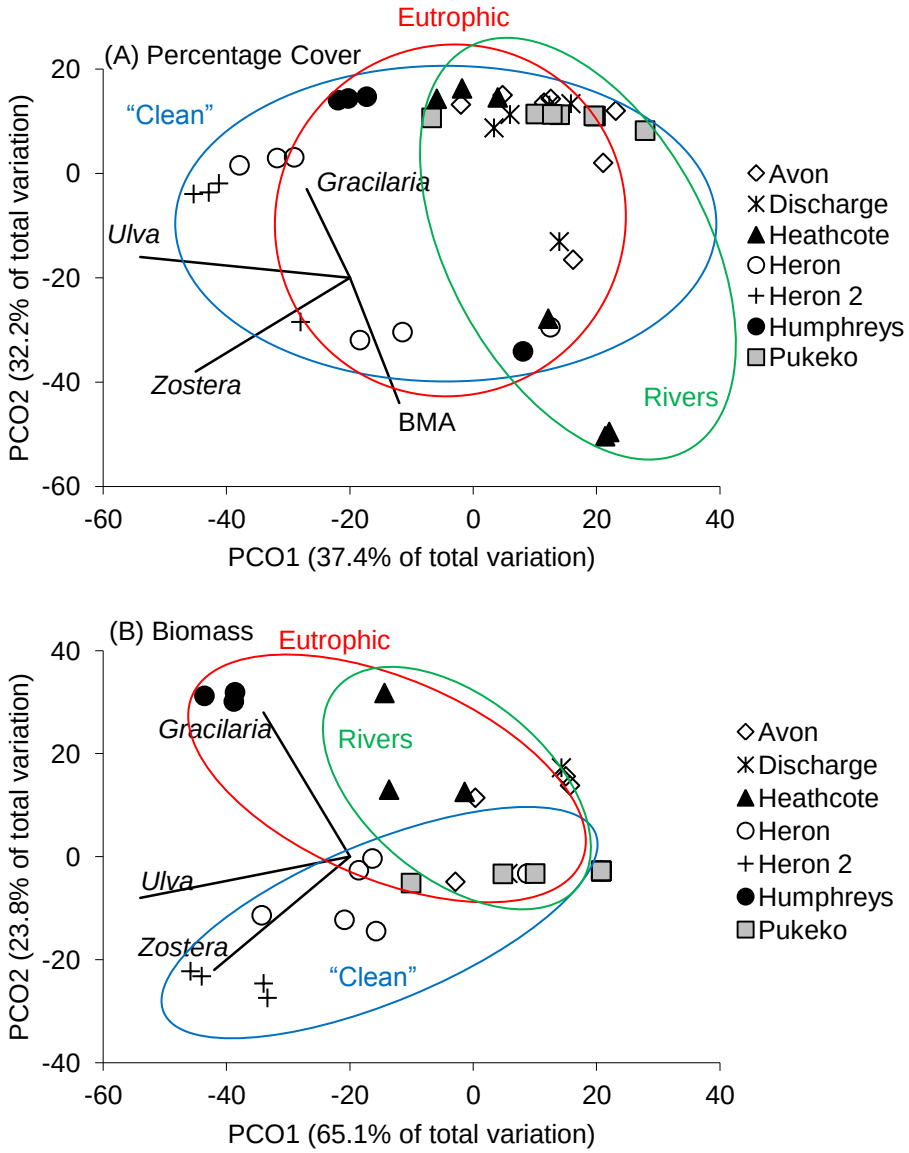

Figure 2.13. PCO plots showing percentage cover of marine plants (A) and biomass of marine plants (B) across seven sites over seven (Avon, Discharge, Heron, Pukeko), six (Heathcote) and five (Heron 2, Humphreys) sampling dates. N=7-15 replicates per site per sampling date. Vectors are shown for Spearman's correlations. "Clean" sites (blue circle) = Heron, Heron 2 and Pukeko, "eutrophic" sites (red circle) = Humphreys and Discharge, and "rivers" (green circle) = Avon and Heathcote.

2.3.4. Fauna associated with marine plants: Case-study at Humphreys

To examine the faunal communities associated with the marine plants, all marine plants collected for biomass at Humphreys were first washed thoroughly to remove the associated organisms. These were subsequently identified and counted.

The community varied through time as it responded to the diversion and earthquakes (Pseudo-F=23.82 $p<0.001$). Taxa richness was greatest at the start of the study where it peaked at 8.3 taxa per gram of marine plants (dry weight) (Fig. 2.14A). This reduced to 4.9 taxa/gram dry weight in February 2010 and, after the earthquakes, this reduced to zero due to the disappearance of marine plants at this site. The number of individuals associated with the marine plant biomass at Humphreys peaked in February 2011 at >1000 individuals per gram of dry weight of marine plants (Fig. 2.14B). Despite relatively high taxa richness in January 2011, only 14.1 individuals were found on average per gram of dry weight of marine plants. Figure 2.15 shows that the community of marine plant associated fauna in December 2009 and January 2011 was influenced more by the abundance of the amphipods *Monocorophium* and *Paracalliope*, as well as *Amphibola*, *Microlenchus* and *Notoacmea*. In contrast, the community in February 2010 appeared to be mainly underpinned by *Macrophthalmus*, *Arthritica* and *Phretogommarus*. SIMPER analysis shows that *Arthritica* contributed >35% to the community across all sampling periods and that in February 2010, only four taxa contributed to >90% of the community composition. In December 2009 and January 2011, there were 8 and 6 taxa contributing respectively (Table 2.5).

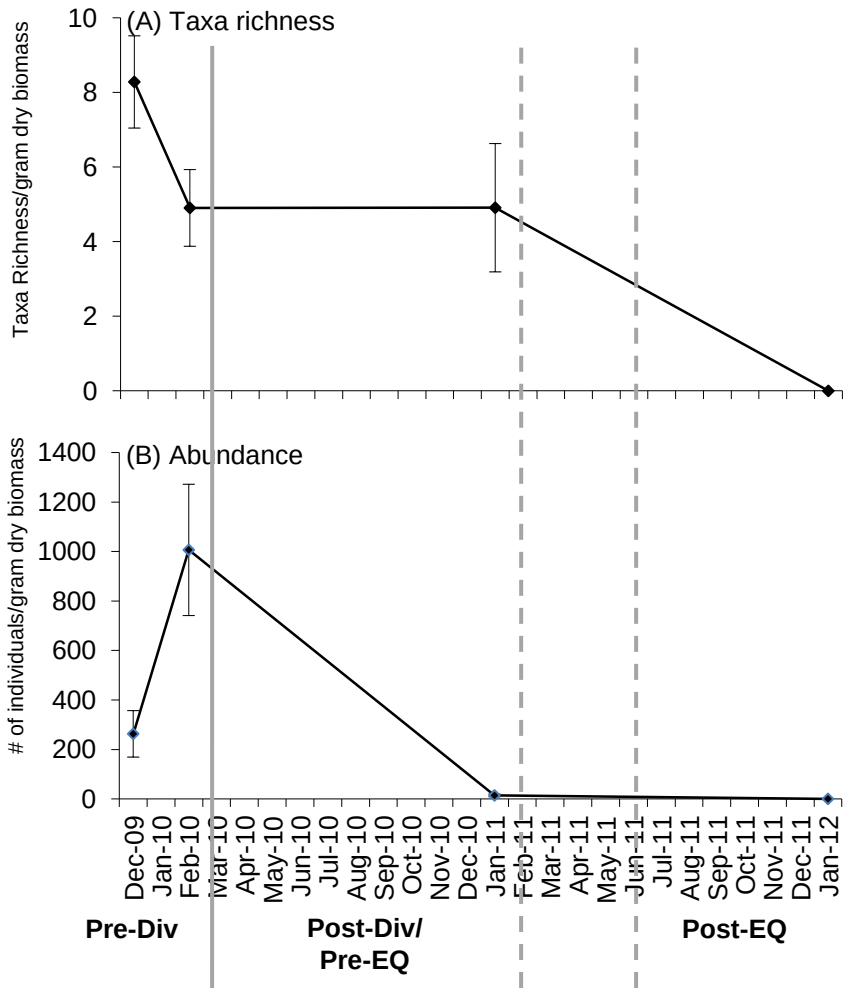

Figure 2.14. Taxa richness (A) and number of individuals (B) for fauna associated with the marine plant biomass at Humphreys over four sampling dates: December 2009, February 2010, January 2011 and January 2012. Results are standardised to taxa richness/number of individuals per gram of dry biomass of marine plants. N=7-15 replicates per site per sampling date.

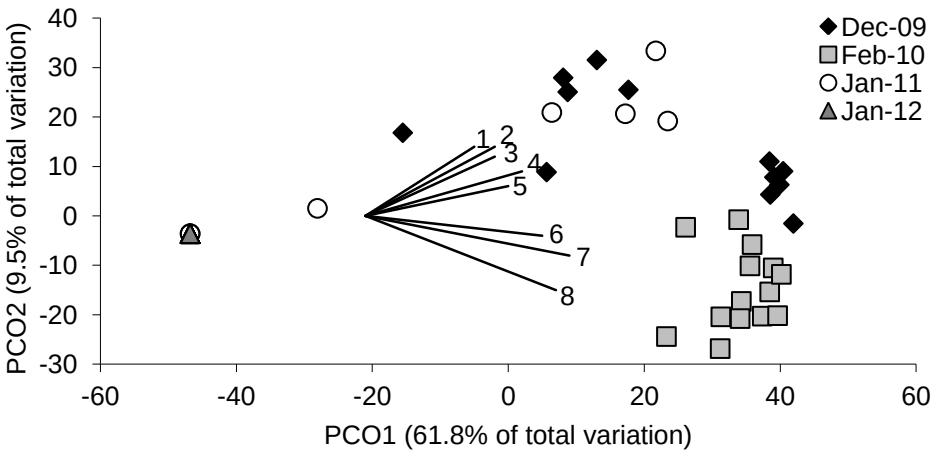

Figure 2.15. PCO plot showing the community composition of the fauna associated with the marine plant biomass at Humphreys over four (December 2009, February 2010, January 2011 and January 2012) sampling dates. N=7-15 replicates per sampling date. Vectors are plotted where Spearman's correlations are >0.6. 1=*Monocorophium*, 2=*Paracalliope*, 3=*Amphibola crenata*, 4=*Microlenchus tenebrousa*, 5=*Notoacmea helmsi*, 6=*Macrophthalmus hirtipes*, 7=*Arthritica*, 8=*Phretogommarus*.

Table 2.5. SIMPER analysis showing marine plant associated fauna contributing to 90% of community at Humphreys during three sampling dates (December 2009, February 2010 and January 2011). Note that no fauna were found in January 2012. N=7-15 replicates per sampling date.

Date	Taxa	Av. Abund	Contrib%
Dec-09	*Arthritica* sp.	2.24	35.93
	Paracalliope	1.93	11.32
	Amphibola crenata	1.01	11.03
	Microlenchus tenebrosus	0.88	9.28
	Phretogommarus	1.52	8.25
	Monocorophium	1.12	8.09
	Macrophthalmus hirtipes	0.86	4.64
	Juv. crab	0.73	4.1
Feb-10	*Arthritica* sp.	4.32	42.98
	Phretogommarus	3.65	32.99
	Macrophthalmus hirtipes	1.5	11.73
	Microlenchus tenebrosus	0.6	2.56
Jan-11	*Arthritica* sp.	1.04	36.22
	Notoacmea helmsi	0.67	23.56
	Hemigrapsus crenulatus	0.56	12.99
	Macrophthalmus hirtipes	0.47	10.1
	Paracorophium	0.31	4.48
	Microlenchus tenebrosus	0.29	3.49

2.3.5. Sediment

The grain size composition of sediments varied by site and also by site x date for the <63µm and >250µm size classes (Table 2.6). In general, smaller grained sediments were more represented at Avon, Discharge, Heathcote and Humphreys and larger grained sediments were commoner at Heron, Heron 2 and Pukeko (Fig. 2.16). There were no clear overall temporal changes across sampling dates and periods but at Humphreys, Heron and Heron 2 there was an increase in the proportion of coarser grained sediments after the February 2011 earthquake.

Sediment organic content differed significantly among sites ($F_{6,157}$=11.20 p<0.001) and there were significant effects of site x sampling period ($F_{12,157}$=3.61 p=0.0076) and site x date(sampling period) ($F_{17,157}$=2.75 p<0.001). These interactions were caused mostly by pre-diversion sediment at Humphreys having significantly greater organic content than sediment at all other time periods from all other sites (Fig. 2.17). Sediments at Avon, Heron, Heron 2 and Pukeko had the lowest organic content overall, with sediments at Discharge and Heathcote having only slightly higher organic content. Greatest temporal variability in organic content occurred at Humphreys and Heathcote whereas Heron, Avon and Pukeko showed little variation over the sampling dates.

Table 2.6. General linear model results examining the effects of site (fixed; 7 levels: Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys and Pukeko), sampling periods (fixed; 3 levels: pre-diversion (December 2009, February 2010), post-diversion/pre-earthquake (July 2010, January 2011), post-earthquake (July 2011, January 2012, July 2012)) and dates nested within sampling periods on sediment grain size. Note that Heron 2 and Humphreys were not sampled in July 2010 and July 2011, and Heathcote was not sampled in December 2009. N=5 samples per sampling date per site. *Cochrans C still significant following log transformation of data and p-value significance reduced to 0.01. N=5 replicates per site per sampling date. Si = site, SP = sampling period, Da = date.

	<63µm			**63-125µm**			**125-250µm**			**>250µm**		
	DF	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**P**
Si	6	37.36	**<0.001**	6	17.31	**<0.001**	6	9.18	**<0.001**	6	8.15	**<0.001**
SP	2	0.062	0.94	2	1.86	0.27	2	2.17	0.38	2	5.11	0.086
Da(SP)	4	3.65	0.027*	4	4.72	0.010*	4	0.21	0.93	4	2.11	0.13
Si*SP	12	0.63	0.79	12	1.99	0.10	12	0.96	0.52	12	2.42	0.051
Si*Da(SP)	16	2.74	**<0.001**	16	1.02	0.44	16	2.01	0.015*	16	3.93	**<0.001**

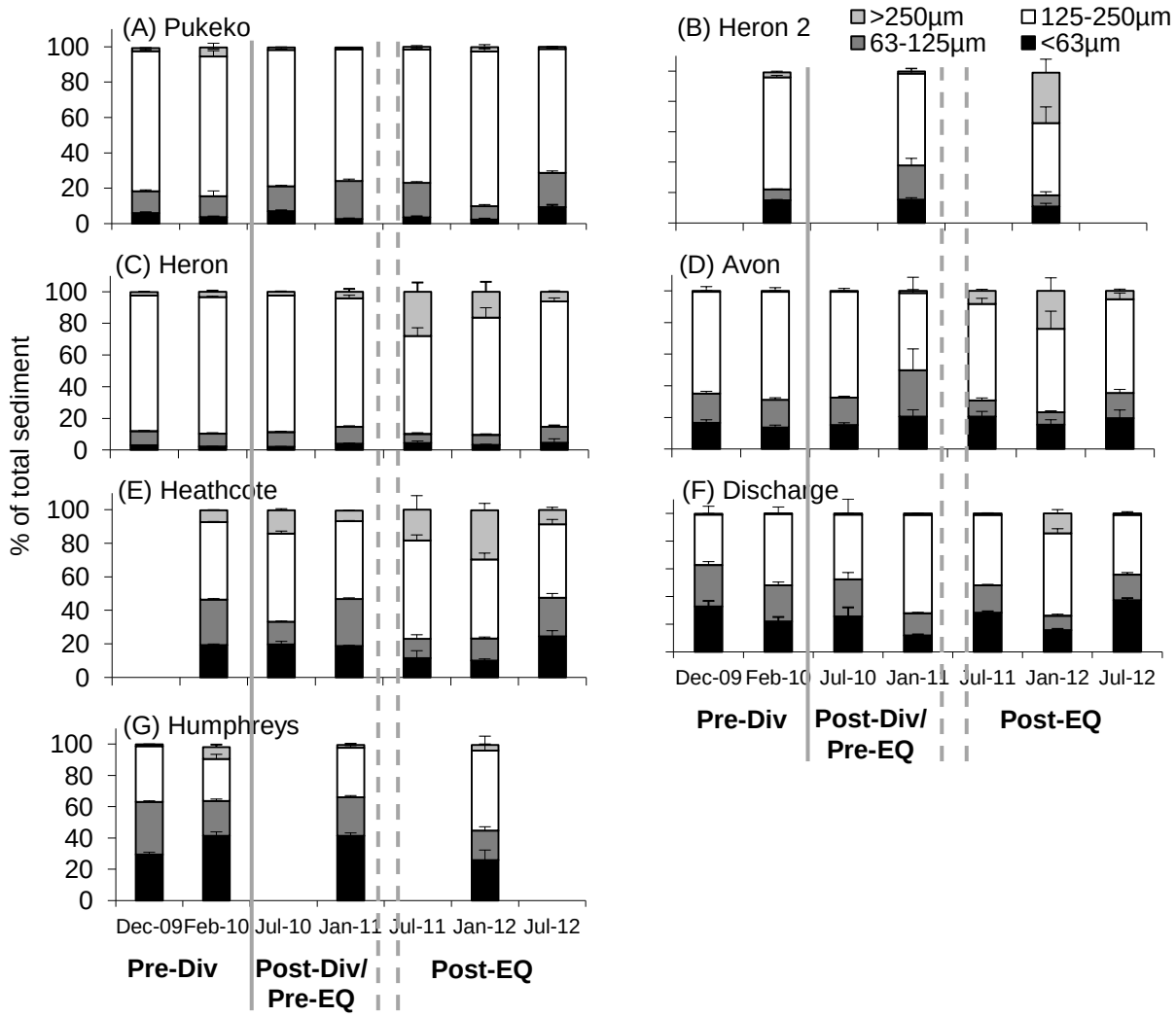

Figure 2.16. Average grain size (+SE) for sediments taken from seven sites (Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys and Pukeko) on sampling dates between December 2009 and June 2012. Solid grey line indicates timing of the diversion (March 2010) and the dashed grey lines show the timing of the February 2011 and June 2011 earthquakes. N=5 replicates per site per sampling date. Sites are ordered in a eutrophication gradient from low (A) to high (G).

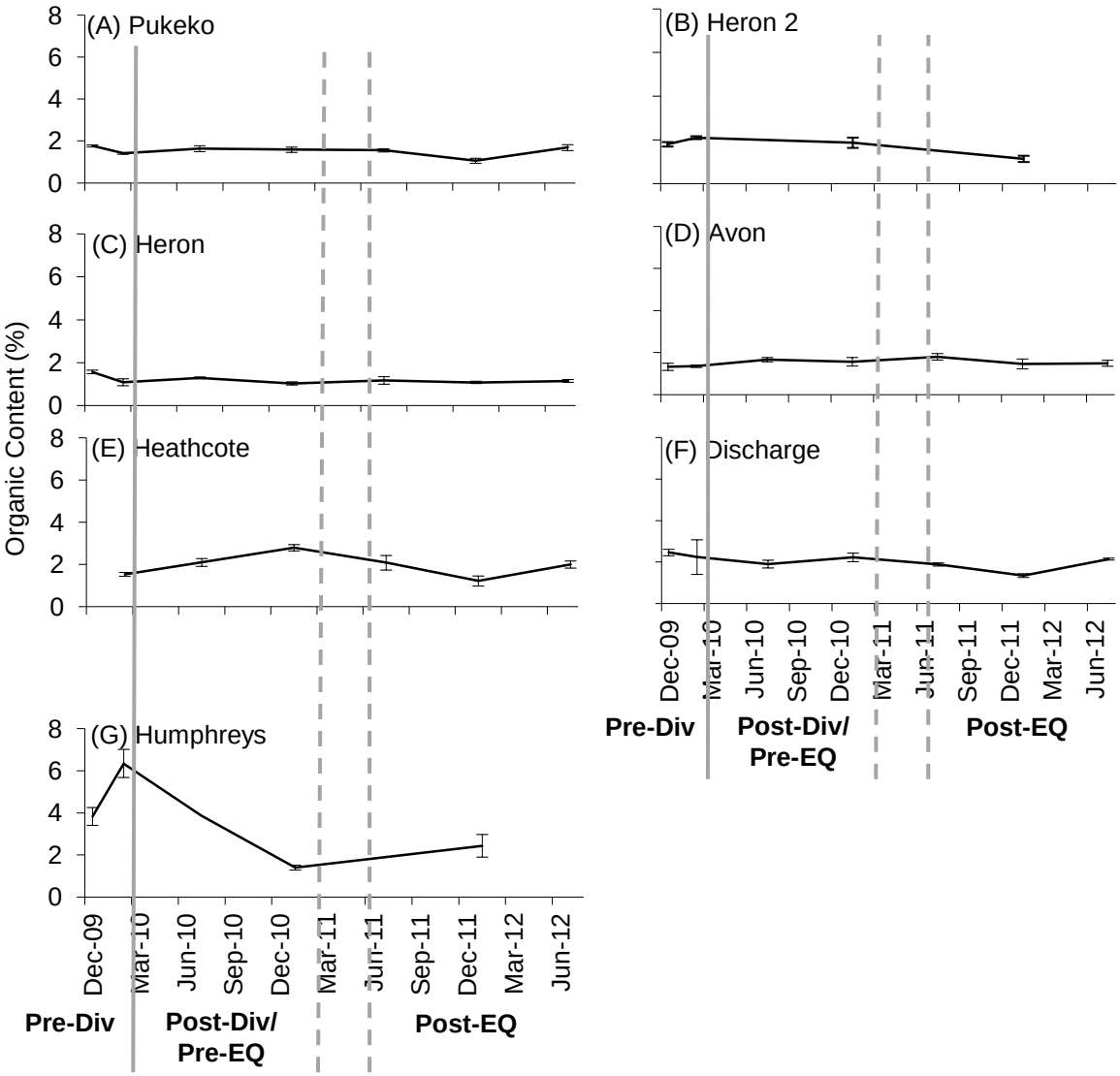

Figure 2.17. Average percentage organic content in sediment samples taken from seven sites (Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys and Pukeko) on sampling dates between December 2009 and June 2012. Solid grey line indicates timing of the diversion (March 2010) and the dashed grey lines show the timing of the February 2011 and June 2011 earthquakes. N=5 replicates per site per sampling date. Sites are ordered in a eutrophication gradient from low (A) to high (G).

DistLM analysis showed that marine plant biomass (pseudo-F=2.66 p=0.011 prop=0.064), marine plant percentage cover (pseudo-F=2.59 p=0.010 prop=0.062) and percentage mud (pseudo-F=4.49 p<0.001 prop=0.10) had significant effects on infaunal community composition. Sequential tests indicated that a combination of all four variables (marine plant biomass, marine plant percentage cover, percentage mud (<63µm) and sediment organic content) provided the best combination to describe infaunal community composition, with an R^2 value of 0.22. Infaunal communities at Heron 2 and Humphreys were most influenced by marine plant biomass and percentage cover whereas communities at Discharge, Avon, Heathcote and Heron were more influenced by percentage mud and the organic content of the sediment (Fig. 2.18A).

Marine plant biomass (pseudo-F=3.78 p=0.012 prop=0.088), marine plant percentage cover (pseudo-F=5.04 p=0.0023 prop=0.11), percentage mud (pseudo-F=6.55 p=0.0002 prop=0.14) and organic content (pseudo-F=3.18 p=0.028 prop=0.075) had significant effects on surface faunal community composition. Sequential tests indicated that a combination of all four variables provided the best combination to describe surface faunal community composition, with an R^2 value of 0.31. Infaunal communities at Heron 2 were most influenced by marine plant biomass whereas communities at Humphreys were more influenced by percentage mud and the organic content of the sediment (Fig. 2.18B).

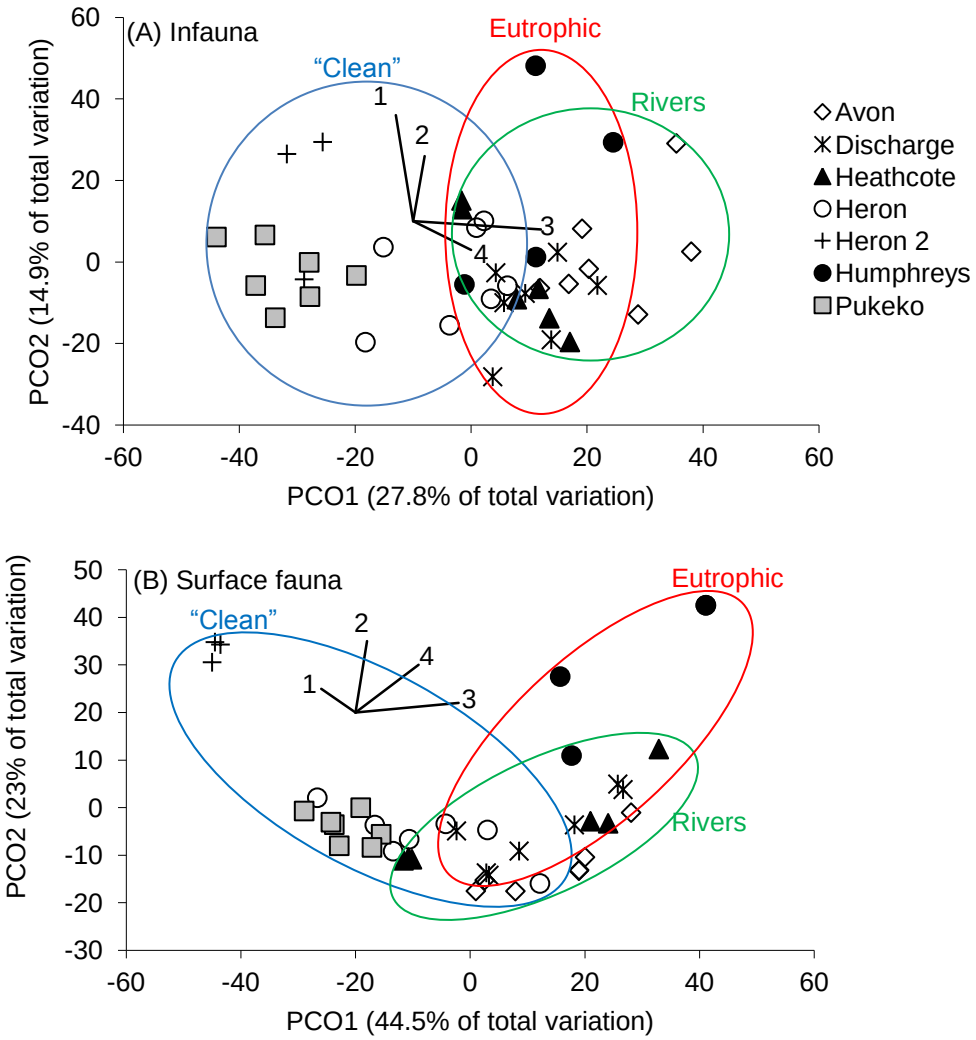

Figure 2.18. PCO plot showing infaunal (A) and surface faunal (B) community composition at seven sites (Avon, Discharge, Heathcote, Heron, Heron 2, Humphreys, Pukeko) over seven sampling dates for Avon, Discharge, Heron and Pukeko (December 2009, February 2010, July 2010, January 2011, July 2011, January 2012, July 2012), six sampling dates for Heathcote (February 2010, July 2010, January 2011, July 2011, January 2012, July 2012) and four sampling dates for Heron 2 and Humphreys (December 2009, February 2010, January 2011, January 2012). Vectors of predictors variables (1=marine plant biomass; 2=marine plant percentage cover; 3=percentage mud (grain size <63µm); 4=sediment organic content) are shown using Spearman's correlations. N=5 replicates per site per sampling date. "Clean" sites (blue circle) = Heron, Heron 2 and Pukeko, "eutrophic" sites (red circle) = Humphreys and Discharge, and "rivers" (green circle) = Avon and Heathcote.

2.4. Discussion

More than 50 years of wastewater input has produced a strong eutrophication gradient within the Avon-Heathcote Estuary. This gradient is related to the proximity of sites to the former discharge pipe from the Bromley Oxidation Ponds and the

hydrodynamic features of different sites. The characteristics of the faunal communities that occurred were related to the pre-diversion eutrophication status of sites. Communities at the eutrophic sites had relatively few taxa with a higher representation of opportunistic taxa. In comparison, communities at the clean sites were more diverse. There was no clear evidence of site-specific temporal changes to invertebrate communities after the diversion and before the earthquakes but this time period was relatively short (11 months). Clearly, the earthquakes altered the natural trajectory of recovery of communities and habitats after the diversion. This too, was spatially variable depending on the amount of liquefaction ("new sediments") and the input of raw sewage received by particular areas after the earthquakes. It must be noted, however, that I did not sample effects of all the site changes because the position of the fixed transects were determined pre-diversion and consequently they missed much of the liquefaction. At Humphreys and Heathcote, two of the most eutrophic sites, large amounts of new sediments fell within the-transect and as such, the nature of changes were localised (i.e., on the scale of centimetres to metres in contrast to among-site changes) due to this patchy habitat. Temporal changes in sediment composition were greatest at these sites and because of the burial/capping (this process is detailed in *Chapter 3*) of eutrophic sediments, long-term recovery of sediments and, in turn, invertebrate communities at these sites may be accelerated relative to the "natural" rate after the diversion (although this is speculative). Note that the term "recovery" can be defined in many ways, but here it is used to indicate that the physical and biological features of the site improve to the state of being similar to those at the least eutrophic sites (Heron 2, Pukeko). A detailed discussion of what ecological end-points constitute a successful ecosystem recovery is covered in *Chapter 6: Overall Summary and General Discussion*.

Recovery rates of soft-sediment communities are influenced by many factors including the size and duration of the disturbance, the structure and dynamics of the ambient community, and habitat features such as sediment composition, flow rates, currents, salinity and oxygen levels (Taylor and Saloman 1969, Kaplan 1975, Jones and Candy 1981, Jones 1986). In particular, eutrophication can affect benthic communities by either increasing food supply, resulting in increased community biomass, or by causing oxygen deficiency, which can reduce community biomass and/or eliminate some species (Josefson 1990, Rosenberg et al. 1992). At the most eutrophic sites, it appears that despite the reduction in nutrient inputs after the

diversion, the legacy effects, such as nutrients stored in the sediments along with high levels of sediment organic content and anoxic cohesive sediments, remained dominant. This occurred despite the addition of new sediments and prevented much change to the largely absent faunal community. As described in *Chapter 3*, new sediments produced by the earthquakes were devoid of fauna when they appeared and the subsequent colonisation of these sediments seemed to be from fauna from neighbouring sediments. At Humphreys, these neighbouring sediments contained very few fauna to at act as colonists. Not surprisingly, Capitellidae was the most abundant taxon at this site. These opportunistic deposit-feeding polychaetes are well known to be pioneering colonists that flourish and dominate assemblages in highly polluted and disturbed areas. The abundance of Capittelidae is closely associated with the nutritive value of the sediment and populations can increase in areas with greater food availability, decayed buried macroalgae, high levels of sediment organic matter and muddier sediments (Lopez and Levinton 1987, Marsh and Tenore 1990, Franke et al. 2006). These conditions describe the relatively high levels of organic content and mud content that were characteristic of the sediments at Humphreys. For example, based on the total organic carbon condition ratings developed for estuaries in Southland New Zealand (e.g., Robertson 2006) the organic content of sediments at Humphreys, which peaked at >6%, was of a poor (>5% organic content) condition. Sediment organic content at this site had, however, reduced considerably by January 2011 which is probably due to the reduction in organic matter entering the estuary after the diversion and less algal detritus after the reduction in algal biomass at this site.

Although invertebrate communities at Humphreys showed little change throughout the study, there was a large change in algal biomass at this eutrophic site. After the diversion, there was a reduction in the amount of *Gracilaria* and by January 2012 it had completely disappeared. The initial reduction occurred during summer when light levels were high but nutrients were far lower than they had been for years. Legacy nutrients stored in the sediments were not enough to sustain the previous prolific growth. After the earthquakes, the site was elevated, reducing the tidal immersion period of the site, nutrients were low and burial of *Gracilaria* was common, as seen in core samples (*Chapter 3*). Furthermore, drift *Gracilaria* do not readily attach to coarse sediments, such as the liquefaction mounds. The large *Gracilaria* bed essentially shifted across the bay, where old sediments persisted.

Before *Gracilaria* disappeared, up to 4.9 taxa and 1006 individuals per gram of dry weight algae were found at Humphreys, supporting other authors who have found clumps of macroalgae to contain large numbers of fauna (Holmquist 1994, Brooks and Bell 2001). In particular, there were high abundances of amphipod species and this is consistent with Ford et al. (1999) who, through experimental manipulation, found that sediments containing algae had a greater number of amphipods than those sediments without algae. For amphipods, the presence of algae represents an increase in food supply and they are highly proficient at increasing their population size opportunistically in response to an increase in resources. The disappearance of nuisance, rotting macroalgae from Humphreys in 2012 may, on one level, seem positive but my results also show that there are important communities associated with these algae which are also lost with its disappearance.

Benthic microalgae became dominant at Humphreys after the disappearance of *Gracilaria* due to the presence of a bare sediment surface in an area of relatively high nutrient availability. Indeed, many authors have found that BMA predominately use nutrients from the sediments, as opposed to the water column, and that they can flourish in areas with high nutrients (e.g., Montgomery et al. 1979, Welsh 1980, Nilsson and Sundback 1991, Underwood et al. 1998, Hutt 2012). But BMA also did well in areas of new sediments (at Heathcote and Humphreys) and this is probably because the coarser new sediments allow for increased solute flux (e.g., increased NH_4-N availability) and increased light penetration which can enhance photosynthetic efficiency (see *Chapter 5*).

Cleaner sites on the eastern side of the estuary (Heron, Heron 2 and Pukeko), are exposed to more dynamic processes such as increased tidal flows and flushing. The sandier and less organically rich sediments found at these sites reflect these processes. Whereas the lowest taxa richness occurred at the eutrophic site of Humphreys, highest faunal taxa richness occurred at Heron 2, reflecting the lower amount of nutrients and pollutants at this site. Heron 2 was the only site where seagrass occurred in any noticeable quantity, a reflection of its relatively clean state (seagrasses have been widely used as indicators of estuarine health (Dennison et al. 1993, Short and Wyllie-Echeverria 1996, Duarte 1999)). In particular, the coarse sediments at this site are suitable for seagrass root attachment and provide a deeper layer of oxygenated sediment. The reduction in *Zostera* after the earthquakes may be due to the close proximity of this site to a large drain, extending from nearby

Plover St, which discharged large quantities of raw sewage into the estuary for 8 months after the February 2011 earthquake (Bolton-Ritchie 2012). Additionally, disruption caused to the sediment by the earthquake events may have dislodged seagrass roots and consequently reduced biomass. The relatively high numbers of taxa found at this site is consistent with many studies that report seagrass meadows as supporting communities that are more diverse and abundant than those in surrounding areas of sediment that do not have seagrass (Stoner 1980, Peterson 1982, Ferrell and Bell 1991, Bostrom and Bonsdorff 1997). This may be due to modifications to the local habitat caused by the physical structure of seagrass, which increases habitat complexity (Edgar and Robertson 1992), reduces water movement (Gambi et al. 1990), traps sediment, larvae and food (Peterson et al. 1984, Bostrom and Bonsdorff 2000), and provides protection (Peterson 1982, Bostrom et al. 2002). The cleanest sites (Heron 2 and Pukeko) were dominated by *Aonides* sp., a genus typically found in coarser sediment. Community composition was less variable over time at these sites because they were less impacted by the diversion and earthquakes. Unlike at Humphreys, Capitellidae did not occur in high abundances at the clean sites, which was probably because of the lower levels of sediment organic matter, pollutants and nutrients, and the coarser sediments.

Much of the *Ulva* and *Gracilaria* accumulation in the estuary is derived from drift of dislodged biomass which grows in other parts of the estuary. Therefore, the abundances and accumulation of biomass at particular sites and not others is due to a complex interaction between estuarine hydrodynamics, wind and wave action, seasonal influences and nutrient availability, both in the sediments and water column (Norkko et al. 2000). The peak of *Ulva* at Heron in February 2010, and its higher biomass at Avon and Pukeko in February 2010 (relative to successive sampling periods at these sites), was probably due to a combination of a summertime algal bloom and higher nutrient availability because of the wastewater entering the estuary. It is well known that *Ulva* proliferates in nutrient-rich environments, particularly during the summer months when there is increased irradiance and warmer temperatures (Valiela et al. 1997, Dan et al. 2002, Villares and Carballeira 2004).

Faunal taxa richness at the river sites (Avon and Heathcote) and two of the clean sites (Heron and Pukeko) were generally similar to each other (and greater than at the eutrophic sites) although there are a couple of interesting points to note.

First, the measure of taxa richness does not necessarily identify changes occurring within the community. For example, there was no change in taxa richness at Discharge after the earthquakes but an analysis of the taxa actually present showed a loss of dominance by the opportunistic Capitellidae at this site and an emergence of new taxa such as *Arthritica* and *Austrovenus* within the community. The community at Discharge is beginning to recover and become more similar to those of less eutrophic sites. Note that there were no new sediments, produced from the earthquake, within the sampled area at Discharge and so the recovery noted here is due to a general improvement of the site in old sediments. A second noteworthy point is that the river sites were the only sites to show a reduction in surface faunal taxa richness after the earthquakes. This was due to liquefaction occurring within the transect at these sites. At Avon, this liquefaction occurred as multiple small discrete areas interspersed with old sediments along the transect. As such, mixing of sediments occurred relatively quickly and surface faunal taxa richness had recovered to pre-earthquake levels by January 2012. In contrast at Heathcote, the entire area of the transect was covered in one large liquefaction mound which persisted throughout the remaining sampling periods. Because of this, it is not surprising that surface invertebrate communities at this site did not recover to pre-earthquake levels by the end of sampling in July 2012.

Summary

The offshore diversion of wastewater from the Avon-Heathcote Estuary provided a unique opportunity to monitor the response of an estuarine ecosystem to nutrient pollution abatement and has provided a valuable spatial and temporal record of ecosystem components through time. Due to the 2011 earthquake events, and the relatively (in recovery terms) short time span of my study, it is difficult to draw general conclusions regarding the impact of the diversion on the ecology and habitats in the Avon-Heathcote Estuary. But I can conclude that, consistent with my hypothesis, there was considerable spatial variability in faunal communities and this was related to the proximity of the sites to the former wastewater discharge pipe and hydrodynamic features. Cleaner sites closest to the estuary mouth, and river sites, had faunal communities that were more diverse than communities at the eutrophic sites. High faunal diversity was associated with the seagrass occurring at Heron 2, whereas the high quantities of *Gracilaria* at Humphreys negatively impacted infaunal

and surface fauna communities, but did show that these algae can support high abundances of amphipod species. As hypothesised, the only obvious earthquake impacts were seen at sites where there were large areas of new sediments occurring within the transect, specifically Heathcote and Humphreys. This may be enhancing the rate of long-term recovery at these sites due to the introduction of large quantities of low nutrient/less organic-rich sediments that have buried significant areas of eutrophic sediments, however, this is conjectural.

Overall, there is some evidence that the wastewater diversion has, so far, been at least partly successful since environmental conditions are improving and polychaete assemblages are becoming more diverse with a reduced abundance of Capitellidae. Although there is still much recovery to go, my results indicate that it is possible to improve even an extremely eutrophied aquatic ecosystem. With increasing numbers of estuaries becoming degraded by pollution and eutrophication worldwide, my results act as an example for environmental managers and decision makers on the timescales and trajectories of the recovery of a highly polluted estuary within the first two-and-a-half years, albeit with the confounding impacts of earthquake events.

Chapter Three

Earthquake-Driven Changes to an Estuarine Ecosystem

3.1. Introduction

Cataclysmic and/or large scale disturbances are generally short, infrequent and unpredictable events that can have considerable effects on the structure and functioning of populations, communities and ecosystems (Lynch 1991, Will 1991, Attiwill 1994, Romme et al. 1998, Turner et al. 1998, Maa et al. 2006). Such disturbances can range from naturally occurring droughts, fires, storms, hurricanes, tornadoes, floods, landslides, ice scour, wave impacts and volcanic eruptions, to anthropogenically induced disturbances like sedimentation, reclamation, dredging, trawling, mass exploitation, atmospheric change (e.g., increased carbon emissions) and mass coral bleaching, all of which vary in intensity, frequency, duration and scale. The biological and ecological effects of disturbances are often species-dependent (Waide 1991, Woolbright 1991, Hughes 1994, Greenberg 2001) and have been shown to reduce the body size (Woolbright 1991, Swilling et al. 1998), breeding behaviour (Jones et al. 2001), distribution (Reagan 1991, Waide 1991, Wunderle et al. 2004), genetic population structure (Apodaca et al. 2013) and survival (Willig and Camilo 1991, Woolbright 1997) of populations. However, there are also studies showing that natural disturbances are important for the regeneration and maintenance of species diversity in some systems (e.g., Salo et al. 1986, Baker 1990, Duncan 1993). Consequently, the resistance and resilience of populations, and the successional changes governing their recovery (detailed in *Chapter 2*) will determine the long-term structure and composition of communities in areas that have undergone disturbances (Romme et al. 1998, Turner et al. 1998).

Numerous studies have performed experimental manipulations (e.g., reducing algae canopy cover on rocky shores (Benedetti-Cecchi et al. 2001); prescribed burning of vegetation (Mazia et al. 2010)) to provide insight into the effects of large-scale physical disturbances on community structure and to understand better the resilience and recovery of communities in both terrestrial and aquatic environments. Due to the unpredictability and low frequency of many large-scale physical natural disturbances however, there are relatively few studies that have examined the effects of these on communities and studies that do, usually focus on short-term changes (Askins and Ewert 1991, Willig and Camilo 1991, Maa et al. 2006). Furthermore, there are only a handful of studies reporting the ecological impact of earthquakes on populations or communities, with such research done across a wide

range of systems, e.g., forests (Wells et al. 2001), streams and rivers (Fang et al. 2002, Lai et al. 2007) and rocky shores (Castilla 1988).

The only known study examining earthquake impacts on communities in an estuarine system is by Maa et al. (2006) who reported the impacts of earthquakes in 1999 and 2002 on insect communities in estuarine mangroves in northern Taiwan. To the best of my knowledge, there are no published studies examining the impacts of large earthquakes on benthic communities in estuarine ecosystems. Consequently, the series of earthquakes that recently occurred in Christchurch New Zealand provided a truly unique opportunity to investigate the impact of such cataclysmic events on estuarine communities and their habitats.

Between 4 September 2010 and 10 January 2012, 3149 earthquakes of magnitude 3 or greater occurred in Canterbury, New Zealand (Geonet 2011). During this period, there were four major earthquakes (Table 3.1). The first and largest earthquake, in September 2010 had the least direct impact on the Avon-Heathcote Estuary because it occurred distant from Christchurch (about 35km to the southwest). Some localised liquefaction (deep sediments pushed up and deposited on the surface - see *Chapter 1: General Introduction* for a full explanation) occurred but this was relatively small and short-lived. Damage to the city's sewage pipes did, however, result in some untreated sewage flowing down the city's Avon and Heathcote Rivers into the estuary for two months after this event (Bolton-Ritchie 2012). Then, the February and June 2011 earthquakes (both of which were much closer to Christchurch) had massive physical effects that included 1) changes in the bed height and inundation profile (Measures et al. 2011), 2) the input of a massive amount (c. 7 billion litres) of untreated sewage/wastewater (Barr et al. 2012), and 3) the appearance of large areas of liquefaction (Zeldis et al. 2011). The December 2011 earthquake had a relatively minimal impact on the estuary.

Table 3.1. Major earthquake events in Christchurch from 2009 to 2012. Note that the December 2011 earthquake was preceded by a 5.9 magnitude tremor that struck at 8km deep and the June 2011 earthquake was preceded by a 6.0 magnitude tremor that struck at 9km deep.

Date	Magnitude (M)	Depth (km)	Relative impact on the estuary
4 Sep 2010	7.1	10	Low
22 Feb 2011	6.3	5	Very High
13 Jun 2011	6.3	6	High
23 Dec 2011	6.0	6	Low

1) Changes in bed height and inundation profile

The February 2011 earthquake caused considerable tilting of the estuary floor (Fig. 3.1). Specifically, the northern side of the estuary, at the Avon River mouth, subsided by 0.2 to 0.5m from its previous level, and the southern side of the estuary, including the estuary mouth and the Heathcote River mouth, lifted by 0.3 to 0.5m (Measures et al. 2011). Overall, the estuary rose by an average of approximately 0.14m and areas exposed at mid-tide increased by an average of 18% over the estuary. This was particularly evident in the south-western side of the estuary. This earthquake resulted in altered tidal flows, tidal heights, channel flows and morphology, within the estuary.

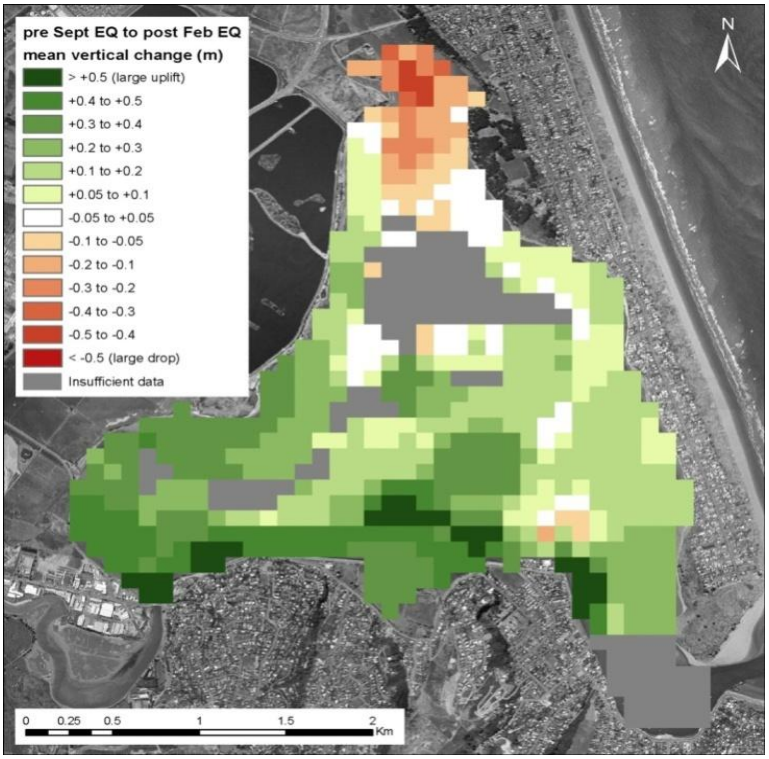

Figure 3.1. Vertical change in the Avon-Heathcote Estuary pre-September 2010 earthquake to post-February 2011 earthquake. Taken from Measures et al. (2011).

2) Input of raw sewage/wastewater

The February 2011 earthquake also caused extensive damage to Christchurch's wastewater reticulation which normally flowed to the Christchurch Wastewater Treatment Plant. As a result, this pipeline was not fully functioning again until 28 October 2011. Untreated sewage and household wastewater entered the estuary through overflows occurring mainly via drains to the rivers, and to a lesser extent

drains flowing directly into the estuary. Untreated sewage and wastewater were received by the estuary via the Avon (~38,000m^3/day initially) and the Heathcote (~27,000m^3/day initially) Rivers. These rates generally decreased over time but untreated sewage and wastewater were discharged into the rivers until 30 July (Heathcote) and 28 September (Avon) 2011 (Bolton-Ritchie 2012). Bolton-Ritchie (2012) reported increased NH_4-N concentrations at sites throughout the estuary from 22 February 2011 until all discharges to the estuary ceased in late October 2011. Prior to the February 2011 earthquake and after the March 2010 wastewater diversion, NH_4-N concentrations at sites throughout the estuary ranged from 0-0.2mg/L but after the earthquake, concentrations at most sites increased 1-3 fold and, at one site, up to 15-fold (Barr et al. 2012).

3) Large areas of liquefaction ("mounds," "new" sediment)

During the February and June 2011 earthquakes, vast areas of the Avon-Heathcote estuary were covered in liquefaction. Initially, liquefaction was seen as numerous mounds created by silt "volcanoes" consisting of sediment pushed to the surface from depth (Fig. 3.2). The June 2011 earthquake produced new mounds and also added more sediment to existing mounds. One of the concerns was that liquefaction may have smothered invertebrate and algal communities or displaced them. The mounds created a considerable amount of new habitat that appeared to be quite different from the surrounding organic-rich "old" sediments. In particular, initial observations indicated that the new sediments were coarser and appeared to be devoid of fauna. These new patches of habitat and the mosaic of old and new sediments within sites, provided an ideal opportunity to examine patterns of colonisation and succession in a large-scale disturbance-recovery context.

The objective of this chapter was to examine the effects of the earthquakes on sediments, seafloor morphology and benthic communities in the estuary, by describing initial post-earthquake conditions and by tracking the trajectory of recovery of each of these components. Specific aims were to 1) quantify new sediment characteristics (percentage cover, height, perimeter), 2) determine initial sediment (grain size, organic content, heavy metals) and biological (marine plants, infauna, surface fauna) differences between old and new sediments, and 3) to identify changes in these variables over spatial and temporal scales.

Figure 3.2. Liquefaction ("new" sediments) at various locations in the Avon-Heathcote Estuary after the 2011 earthquakes

I hypothesised that the new sediments would have lower levels of heavy metals and organic matter initially. Levels of organic matter, sampled over time, were expected to increase in new sediments due to mixing with the surrounding old sediments and new organic matter loading and formation in the estuarine system. It was expected that mixing would also make new sediments muddier and old sediments coarser. In new sediments, taxa richness and the abundance of both infauna and surface fauna were expected to be low initially (with initial populations dominated by opportunistic species) and then increase over time, due to colonisation by fauna in neighbouring old sediments, until an equilibrium was reached.

3.2. Methods

Sampling was done at six sites across the Avon-Heathcote Estuary: Avon, Discharge, Heathcote, Heron, Humphreys and Plover. For location details and a full description of the site characteristics see *Chapter 1: General Introduction*. Briefly, Discharge was a eutrophic site situated below the former discharge pipe of the Bromley Oxidation Ponds which, prior to March 2010, discharged approximately 500,000m^3 of wastewater into the estuary every day (URS 2004). This was one of the main sites for sewage entering the estuary after 22 February 2011. Humphreys is situated in a low-flow "back-water" area about 0.5km from Discharge. Historically, it

also received high amounts of sewage-derived nitrogen from the adjacent Discharge site. Because of low tidal flows and circulation at this site, and its history of supporting the largest *Ulva* and *Gracilaria* biomasses in the estuary (Bolton-Richie 2005), the sediments had accumulated high amounts of organic matter and legacy nitrogen (Zeldis et al. 2011). Avon and Heathcote are estuarine sites near their respective river mouths and consequently are exposed to greater amounts of riverine inputs. Large amounts of sewage and wastewater entered the estuary via these rivers after the earthquakes. Heron and Plover are situated nearest the estuary mouth. These were the least eutrophic of all sites before the earthquakes. After 22 February 2011, large quantities of raw sewage flowed across Plover pumped from an adjacent broken urban sewage main, directly onto the intertidal zone affecting this site and potentially Heron.

Due to logistical constraints and the generally difficult circumstances that follow a natural disaster of this scale, sampling of new sediments was not able to begin until 30-70d (site dependent) after the 22 February 2011 earthquake. After the 13 June 2011 event, however, sampling of the new sediments produced by this earthquake began within 48h. New sediments produced by the June earthquake were easy to distinguish from those that were produced in February due to “ripples” on fresh mounds and the absence of benthic microalgae (BMA). Consequently, for nearly all physical and biological variables, two data sets were obtained: one was from sampling new sediments which were produced by the 22 February 2011 earthquake and the other from sampling new sediments which were produced by the 13 June 2011 earthquake (Table 3.2). Sampling was done at all six sites for new sediments that appeared during the February event and at four sites (Avon, Heathcote, Humphreys and Plover) for new sediments that appeared during the June event. This was due to an inadequate presence of new sediments at the remaining two sites after the June earthquake. The February and June earthquake data sets were not combined for graphing and analytical purposes due to the impacts of different seasonal dynamics, an unequal number of sites and varying amounts of time occurring between the earthquake and the first sampling period after the February and June events.

Table 3.2. Dates and sites where sampling was done after the 22 February 2011 (A) and 13 June 2011 (B) earthquakes

(A) Feb-11 EQ

Sampling Type	Sites	First Sampling Date (Days after EQ)	Dates Re-sampled
% cover of new sediments	Avon	2/5/11 (70)	Jun-11
	Discharge	24/3/11 (31)	Jun-11
	Heathcote	29/4/11 (67)	Jun-11, Sep-11
	Heron	28/3/11 (35)	Not re-sampled
	Humphreys	25/3/11 (32)	Jun-11, Sep-11
	Plover	3/5/11 (71)	Jun-11, Sep-11
New sediment height	Avon	2/5/11 (70)	Approx. monthly until Jul-12 at all sites
	Discharge	24/3/11 (31)	
	Heathcote	29/4/11 (67)	
	Heron	28/3/11 (35)	
	Humphreys	25/3/11 (32)	
	Plover	3/5/11 (71)	
New sediment perimeter	Avon	2/5/11 (70)	Jun-11, Sep-11, Oct-11
	Discharge	24/3/11 (31)	Jun-11, Sep-11, Oct-11
	Heathcote	29/4/11 (67)	Jun-11, Sep-11, Oct-11
	Heron	28/3/11 (35)	Not re-sampled
	Humphreys	25/3/11 (32)	Jun-11, Sep-11, Oct-11
	Plover	3/5/11 (71)	Jun-11, Sep-11, Oct-11
% cover of marine plants, surface fauna, infauna, surface sediments (grain size and organic content)	Avon	2/5/11 (70)	Sep-11, Dec-11, May-12
	Discharge	24/3/11 (31)	Sep-11, Dec-11, May-12
	Heathcote	29/4/11 (67)	Sep-11, Dec-11, May-12
	Heron	28/3/11 (35)	Jun-11, Sep-11, Dec-11, May-12
	Humphreys	25/3/11 (32)	Sep-11, Dec-11, May-12
	Plover	3/5/11 (71)	Sep-11, Dec-11, May-12
Surface sediment heavy metal content	Avon	2/5/11 (70)	Not re-sampled at any site
	Discharge	24/3/11 (31)	
	Heathcote	29/4/11 (67)	
	Heron	28/3/11 (35)	
	Humphreys	25/3/11 (32)	
	Plover	3/5/11 (71)	
Long sediment cores	Avon	2/5/11 (70)	Sep-11, May-12
	Discharge	24/3/11 (31)	Sep-11, May-12
	Heathcote	29/4/11 (67)	Sep-11, May-12
	Heron	28/3/11 (35)	Sep-11, May-12
	Humphreys	25/3/11 (32)	Sep-11, May-12
	Plover	3/5/11 (71)	Sep-11, May-12

(B) Jun-11 EQ

Sampling Type	Sites	First Sampling Date (Days after EQ)	Dates Re-sampled
New sediment height	Avon	20/6/11 (6)	Approx. monthly until Jul-12
	Heathcote	17/6/11 (4)	Approx. monthly until Jul-12
	Humphreys	17/6/11 (4)	Approx. monthly until Nov-11
	Plover	20/6/11 (6)	Approx. monthly until Jul-12
New sediment perimeter	Avon	20/6/11 (6)	Sep-11, Oct-11
	Heathcote	17/6/11 (4)	Sep-11, Oct-11
	Humphreys	17/6/11 (4)	Sep-11, Oct-11
	Plover	20/6/11 (6)	Sep-11, Oct-11
% cover of marine plants, surface fauna, infauna, surface sediments (grain size and organic content)	Avon	20/6/11 (6)	Sep-11, Dec-11, May-12
	Heathcote	17/6/11 (4)	Sep-11, Dec-11, May-12
	Humphreys	17/6/11 (4)	Sep-11, Dec-11, May-12
	Plover	20/6/11 (6)	Sep-11, Dec-11, May-12

3.2.1. Field methods

3.2.1.1. Cover of new sediments

To examine the percentage cover of new sediments, four 30m fixed transects were randomly positioned and permanently marked at each site. These ran parallel to each other and were in the mid tidal region. The proportion of old and new sediments

was recorded at 1cm distances along each transect. This sampling was repeated in June 2011 (after the earthquake) and September 2011 or until it became too difficult to accurately differentiate the boundaries between old and new sediments.

3.2.1.2. Height and perimeter of new sediments

To determine the height of areas of new sediment relative to the old estuary floor sediments, five mounds were randomly selected at each of the six sites after the February 2011 earthquake. The height of each mound was measured using a spirit level with an attached laser. The level and laser were positioned on the highest point of each mound (marked with a stake during the initial sampling date), kept level, and the laser pointed at a ruler held vertically on the surrounding old sediment. Re-measurement of the same five mounds was done approximately monthly from March 2011 to June 2012 (Table 3.2). Five new mounds were measured at Avon, Heathcote, Humphreys and Plover after the June event. Their heights were also measured approximately monthly until June 2012.

To calculate the area of mounds, their perimeters were measured by running a measuring tape around them. Mounds were re-sampled twice or until it became too difficult to differentiate the edges of old and new sediments.

3.2.1.3. Marine plants, surface fauna, infauna and surface sediments

To examine differences in marine plant and faunal communities between old and new sediments, labelled markers were placed in the centre of five mounds and five old sediment patches at each site. These were the same old and new sediment areas measured for height and perimeter. A 0.5m x 0.5m quadrat was positioned beside each marker on the old and new sediments and the abundances of different taxa present within the quadrat were recorded. This included both surface fauna (>0.5cm length occurring in the top 0.5cm of sediment) and the percentage cover of different taxa of marine plants (algae and seagrass). A sediment core (20cm length; 9cm diameter) was taken from each area of old and new sediment for the collection of infauna. Note that “infauna” here also includes any epifauna present within a sediment core. The positions of extracted infauna cores were noted to avoid re-sampling these areas on future sampling occasions.

Cores were sieved on a 500µm mesh and the retained infauna stored in 70% ethanol. In the laboratory, infauna were identified to the lowest practical taxonomic

level, which was generally to family and often to genus and species. Precision at these taxonomic levels have been reported as sufficient for resolving community patterns (Agard et al. 1993, James et al. 1995) and reflecting species-level biodiversity in similar habitats (Gaston 2000, Olsgard et al. 2003). The abundance of each taxon in each sample was recorded.

In addition to the sediment sampling described below in *3.2.1.4.*, a surface (<2cm depth) scraping of sediment was also collected from each area of old and new sediment for the analysis of grain size and organic content. The sediment samples were stored on ice and frozen at -20°C pending analysis (described below in *3.2.2.*). As shown in Table 3.2, for new sediments produced by the February 2011 earthquake, sampling of these components occurred on four occasions (April/May 2011, September 2011, December 2011, May 2012) at six sites (Avon, Discharge, Heathcote, Heron (plus additional sampling in June 2011), Humphreys and Plover). For areas of new sediment created by the June 2011 earthquake, sampling occurred on four occasions (June 2011, September 2011, December 2011, May 2012) at four sites (Avon, Heathcote, Humphreys, Plover).

Additional surface sediment scrapings for the analysis of heavy metal content were collected from three areas of new sediment and three areas of old sediment at Avon, Discharge, Heathcote, Heron, Humphreys and Plover during the first sampling occasion after the February 2011 earthquake (Table 3.2).

3.2.1.4. Vertical sediment cores

Three sediment cores (c. 70cm in length) were taken from areas of old and new sediment at each of the six sites (Fig. 3.3). For cores taken from old sediment, samples (c. 80g) were collected from the core surface, 30cm below the surface and 60cm below the surface. For cores taken from new sediments, sediment samples were collected from the surface, the “old sediment surface” (a distinct layer that was generally apparent showing where the new sediment stopped and the old sediment began; Fig. 3.4), 30cm below the old surface, and 60cm below the old surface. All cores were photographed and stratum/sediment layers noted. The sediment samples were stored on ice and frozen at -20°C for organic content and grain size analysis. Sampling was done on three occasions at each site: April/May 2011, September 2011 and May 2012 (Table 3.2).

Figure 3.3. Long core used to sample the vertical profile of sediment from areas of old and new sediment

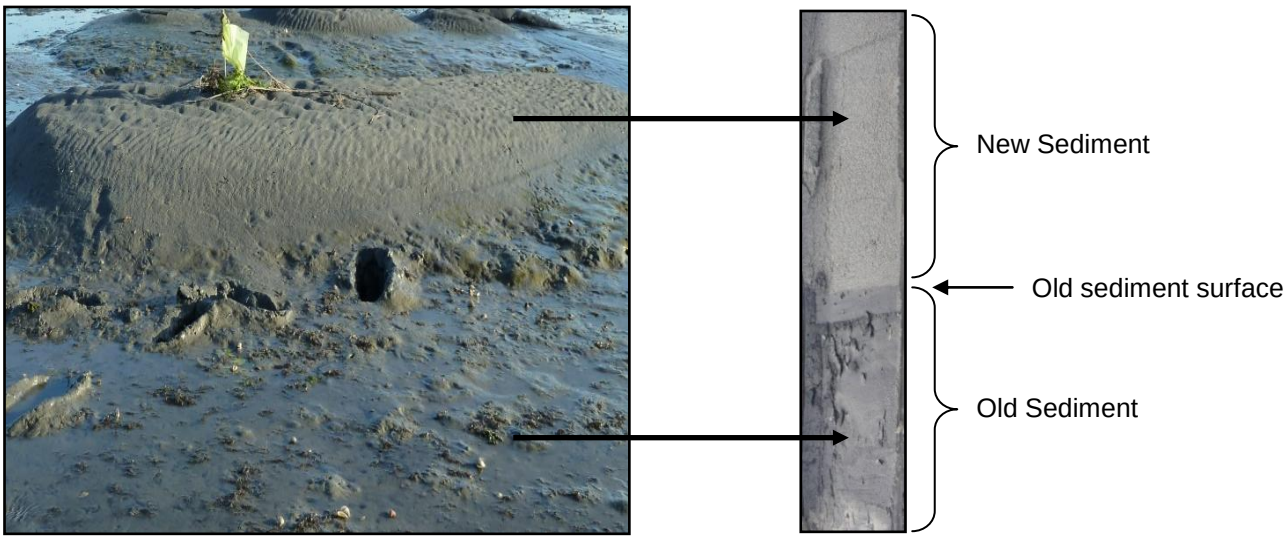

Figure 3.4. Photograph of a long sediment core showing the new sediment (top) and old sediment (below) separated by a distinct boundary layer, the “old sediment surface”

3.2.2. Laboratory methods

To determine the organic content of sediment samples, sub-samples were dried (60°C for 3d) and then combusted (550°C for 5h). The organic content was calculated by subtracting the combusted weight from the dry weight and this was expressed as the percentage of sediment dry weight.

Additional sub-samples were wet or dry sieved through a series of sieves (500µm, 250µm, 125µm, 63µm) to determine the fraction of sediment in each size class (250-500µm = medium sand, 125-250µm = fine sand, 63-125µm = very fine sand, <63µm = silt). Although the sieving technique was not consistent among

samples (wet versus dry), comparisons between these methods showed negligible differences in outputs (see *Chapter 2* for details).

Sediment samples for the analysis of heavy metal content were stored on ice and delivered to Hills Laboratory Christchurch for analysis of total recoverable Arsenic (As), Cadmium (Cd), Chromium (Cr), Copper (Cu), Lead (Pb), Nickel (Ni) and Zinc (Zn). Samples were air dried at 35°C and sieved to separate the <2mm fraction, which was digested using Nitric/Hydrochloric acid.

3.2.3. Statistical analyses

As covered at the beginning of the *Methods* section, two temporal and spatial data sets were collected for most of the physical and biological variables examined and these have been graphed and analysed separately.

Univariate analyses were performed on each of the physical variables (percentage cover of new sediments, new sediment height/perimeter, sediment heavy metal content, sediment organic content and sediment grain size). General linear models (GLMs) were used in each case, with the physical variable as the response and sediment type (fixed; 2 levels: old and new), site (fixed; 6 levels: Avon, Discharge, Heathcote, Heron, Humphreys, Plover) and, where applicable, date (random), as categorical predictor variables. Site was considered a fixed factor as it represented a eutrophication and disturbance gradient. Where necessary, data were log-transformed to fulfil the assumptions of the model and where Cochran's test for homogeneity of variances remained significant following data transformation, p-values were made more conservative by reducing the significance threshold from 0.05 to 0.01 (Underwood 1997). Tukey post-hoc tests were performed to examine significant relationships further. To reduce the complexity of the analyses for the sediment organic content and grain size data sets, only data collected from the initial and final sampling dates were included in the model. Finer scale temporal changes are still shown graphically.

For the biological variables (percentage cover of marine plants and numbers of surface fauna and infauna), data were fourth-root transformed and a resemblance matrix constructed using Bray-Curtis measure of similarity. Permutation analysis of variance (PERMANOVA) were performed with the factors sediment type (fixed), site (fixed) and date (random). For the marine plant and surface fauna analyses, an additional factor of quadrat (fixed and nested within site) was included in the model

to address the issue of repeated measures. Quadrats for surface fauna and macroalgae were positioned to cover exactly the same patch of sediment during every sampling period. Infauna data was treated as independent as unlike quadrats, cores were randomly positioned within old and new sediment patches on each sampling occasion. SIMPER analyses, to identify species driving spatial and temporal differences, were performed for each biological variable. For surface fauna and infauna, the taxa richness and number of individuals between sediment types, among sites and over sampling dates were calculated. Principle Coordinate Ordination (PCO) plots based on distance from centroid data were produced separately for infauna and surface fauna at each site to show the trajectory of change of average community composition across the sampling dates.

Relationships between the percentage mud content of surface sediment and taxa richness and number of individuals were visualised using scatterplots for both infauna and surface fauna.

Following the analysis of individual datasets, multidimensional scaling (MDS) plots were produced with Spearman's vectors overlaid to show the predictor variables (individual heavy metals, organic content and mud content) driving differences in infaunal and surface faunal community composition among sites after the February 2011 earthquake.

Community analyses were performed using PRIMER6 & PERMANOVA and GLMs performed using STATISTICA 7.

3.3. Results

3.3.1. New sediments: Percentage cover, height and perimeter

There was a significant site x date interaction effect ($F_{6,42}$=3.48 p=0.007) on changes in the percentage cover of new sediments with new sediments initially comprising 30 – 65% of the estuary surface across all sites (Fig. 3.5). Heron (50% new sediments) and Avon (65% new sediments) had the highest proportions of new sediments initially but the areas covered with new sediment were less distinct at these sites. Here, they were shallower and blended more into the surrounding old sediments and old and new sediments were more difficult to distinguish from each other. Because of this, sampling ceased prior to September 2011 at these sites. Over the first two sampling dates, Avon showed an almost 50% reduction in the percentage of new sediments. This may have been due to the increased inundation at this site from the

water flow of the Avon River. Increases in the percentage of new sediments at Humphreys and Heathcote between the first and second sampling dates were due to the introduction of more sediments from the June 2011 earthquake.

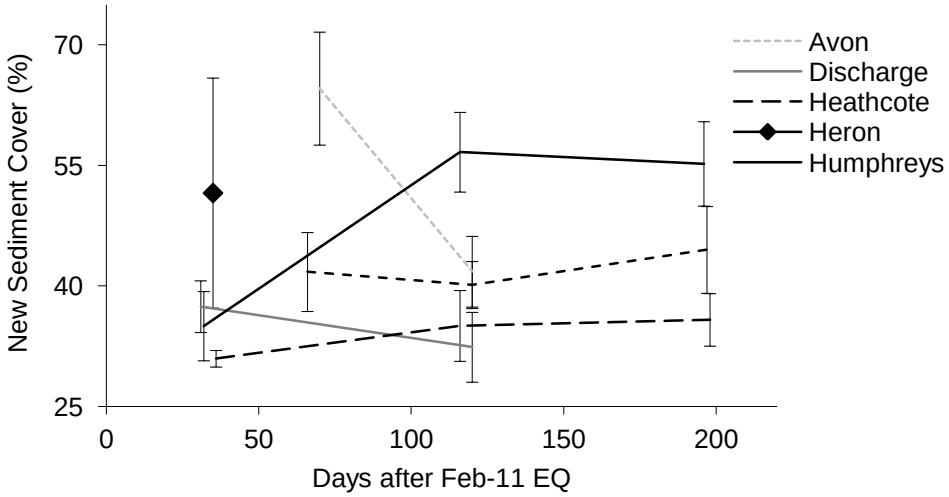

Figure 3.5. Average (±SE) percentage of the estuary surface covered by new sediments at six sites (Avon, Discharge, Heathcote, Heron, Humphreys, Plover) on 1-3 sampling dates (April/May 2011, June 2011 and September 2011) after the February 2011 earthquake. N=4 transects per site per sampling date.

For new sediments produced by the February 2011 earthquake, heights varied significantly among sites ($F_{5,248}$=4.05 p<0.001), dates ($F_{10,50}$=4.00 p<0.001) and the interaction effect was significant ($F_{50,248}$=2.61 p<0.001). Immediately after this earthquake, new sediments were highest at Humphreys and Discharge, and lowest at Avon and Plover (Fig. 3.6A). After the June 2011 earthquake, an increase in the heights of these new sediments was seen at Humphreys, Heathcote, Avon and Plover due to the addition of new sediments produced by this earthquake. Over time, the heights of new sediments at all sites decreased with the largest reduction occurring at Humphreys.

For new sediments produced by the June 2011 earthquake, the initial heights varied significantly among sites ($F_{3,16}$=14.92 p<0.001) with new sediments at Heathcote and Humphreys being significantly higher than new sediments at Plover and Avon (Fig. 3.6B). For Heathcote, Avon and Plover, where measurements continued for >400d, there was a significant effect of site ($F_{2,110}$ =14.28 p<0.001) and date ($F_{9,18}$=6.63 p<0.001) on new sediment height but the interaction effect was not significant ($F_{18,110}$=0.89 p=0.59). Similar to the patterns described for the new

sediments produced by the February 2011 earthquake, heights at all sites decreased over time, with the largest height reductions occurring at Humphreys and Heathcote.

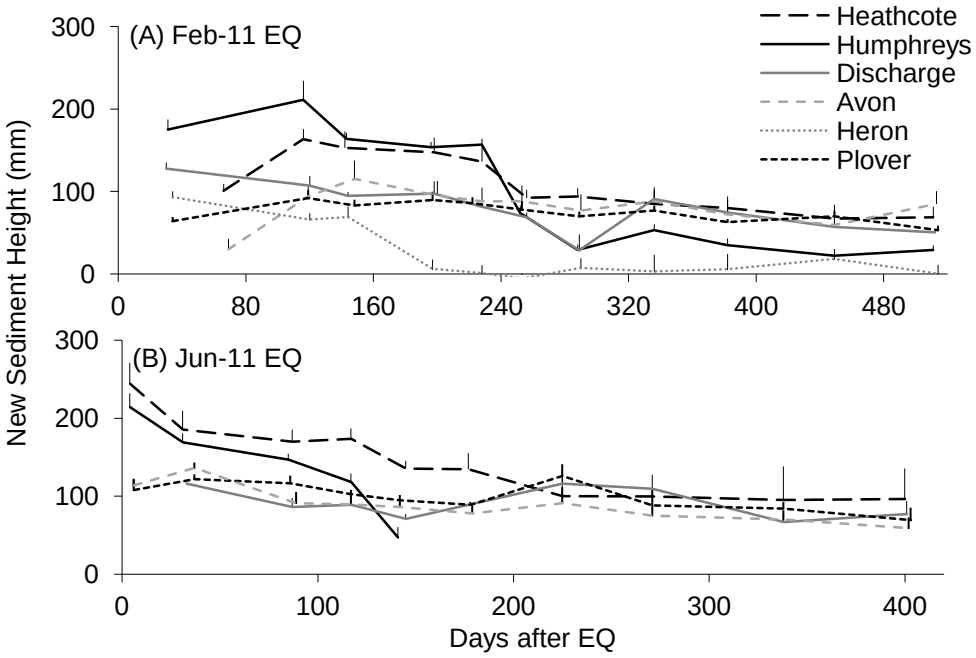

Figure 3.6. Average (+SE) height of marked patches of new sediment on sampling dates between March 2011 and July 2012 (A) and June 2011 and July 2012 (B) for new sediment produced by the February 2011 (A) and June 2011 (B) earthquakes. N=5 replicate areas of new sediment per sampling date per site.

After the initial sampling date, perimeters of new sediments produced by the February 2011 earthquake varied significantly among sites ($F_{5,24}$=3.10 p=0.027), with the largest recorded at Heathcote (15.1m) and Heron (13.6m), and smallest at Discharge (9.1m) and Humphreys (9.5m) (Fig. 3.7A). For analyses performed on all sites except Heron (where measurements could not be accurately continued beyond the initial sampling date due to difficulties distinguishing between old and new sediments), there remained a significant site effect ($F_{4,74}$=13.62 p<0.001) but there were no significant sampling date or interaction effects (both p>0.05).

Similarly, for new sediments produced by the June 2011 earthquake, there was also a significant site effect ($F_{3,42}$=22.62 p=0.001) but no significant sampling date or interaction effects (p>0.05) on the perimeters of new sediments. For these areas of new sediment, the largest and smallest perimeters also occurred at Heathcote (13.5m) and Humphreys (7.8m) respectively (Fig. 3.7B).

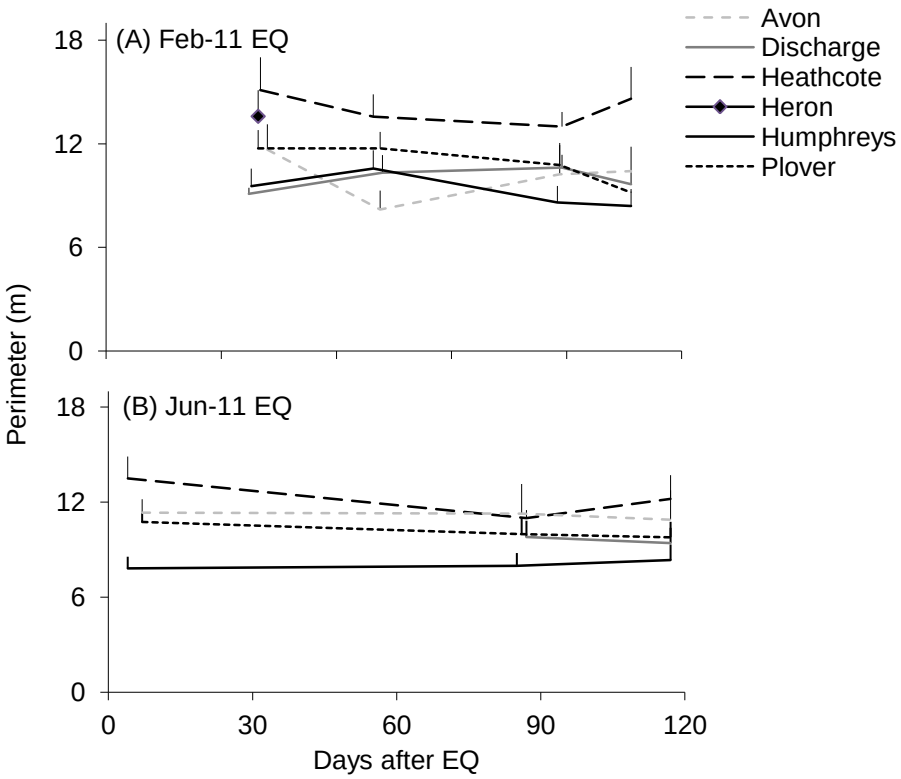

Figure 3.7. Average (+SE) perimeter of marked patches of new sediment on sampling dates between March 2011 and July 2012 (A) and June 2011 and July 2012 (B) for new sediment produced by the February 2011 (A) and June 2011 (B) earthquakes. N=5 replicate areas of new sediment per site per sampling date.

3.3.2. Sediment chemistry and composition

Heavy metal concentrations were usually much greater in old sediments than in new sediments but this varied by site (Fig. 3.8). Effects of site, sediment type and their interaction were highly significant ($p<0.002$) for every heavy metal. Across the seven metals, differences between old and new sediments were always not significant at Plover and Heron and, occasionally, not significant at Discharge and Heathcote. However, in no case, were metal concentrations greater in new sediments than in old sediments.

There were significant site x sampling date x sediment type interaction effects for the organic content of old and new sediments sampled over time after both the February 2011 ($F_{5,67}=4.26$ $p=0.002$) and June 2011 ($F_{3,52}=4.52$ $p=0.007$) earthquakes. In general, there was considerably more organic matter in the surface layer of the old sediments than in the surface layer of the new sediments immediately after the two earthquakes (Figs. 3.9 and 3.10). During the first sampling date after each earthquake, the amount of organic matter in new sediments was

fairly low and consistent among sites. There was, however, greater spatial variation in the organic content of old sediments. In particular, old sediments at Humphreys had very high levels of organic content particularly after the February 2011 earthquake. In general, over the successive sampling dates, the organic content of old and new sediments became more similar within sites due to new and old sediments becoming more and less enriched respectively.

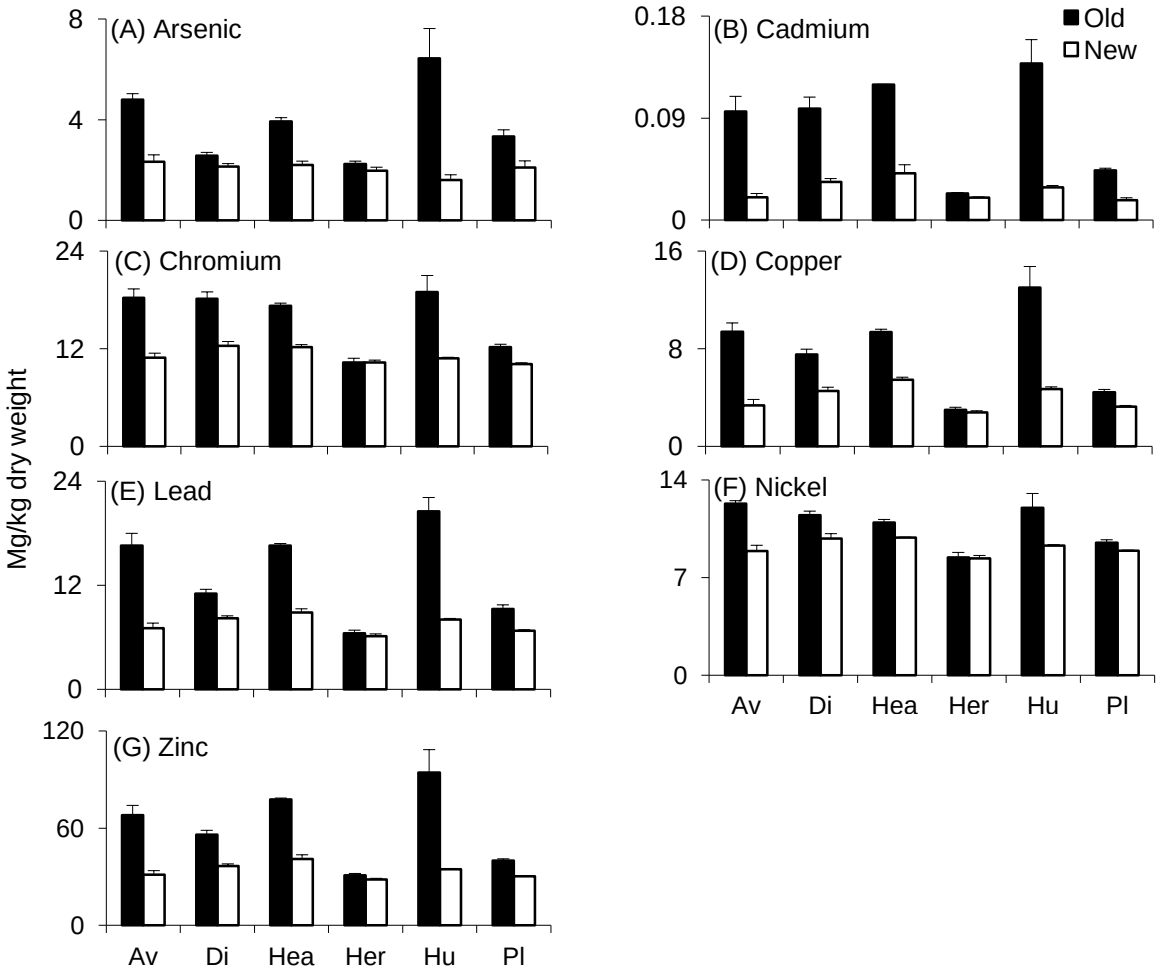

Figure 3.8. Average (+SE) total recoverable heavy metal concentrations for seven heavy metals (A-G) in old and new sediments produced by the February 2011 earthquake at six sites (Avon (Av), Discharge (Di), Heathcote (Hea), Heron (Her), Humphreys (Hu) and Plover (Pl)) after the February 2011 earthquake. N=3 replicates per sediment type per site.

Sediments analysed for organic content from the vertical cores showed that there were no significant differences between the organic content of the surface of the old sediments and the old surface under the new sediments (i.e., what used to be the surface prior to the earthquake) within a site (Table 3.3). Sediment samples taken at 30 and 60cm also showed no differences between the organic content of old and new sediments within each of these depths. There were, however, significant

differences among sites for sediments taken at all depths except the surface and 30cm. Across sites, the organic content of new and old sediments at the surface, 30 and 60cm were similar and low, generally from 1-3% (Fig. 3.11).

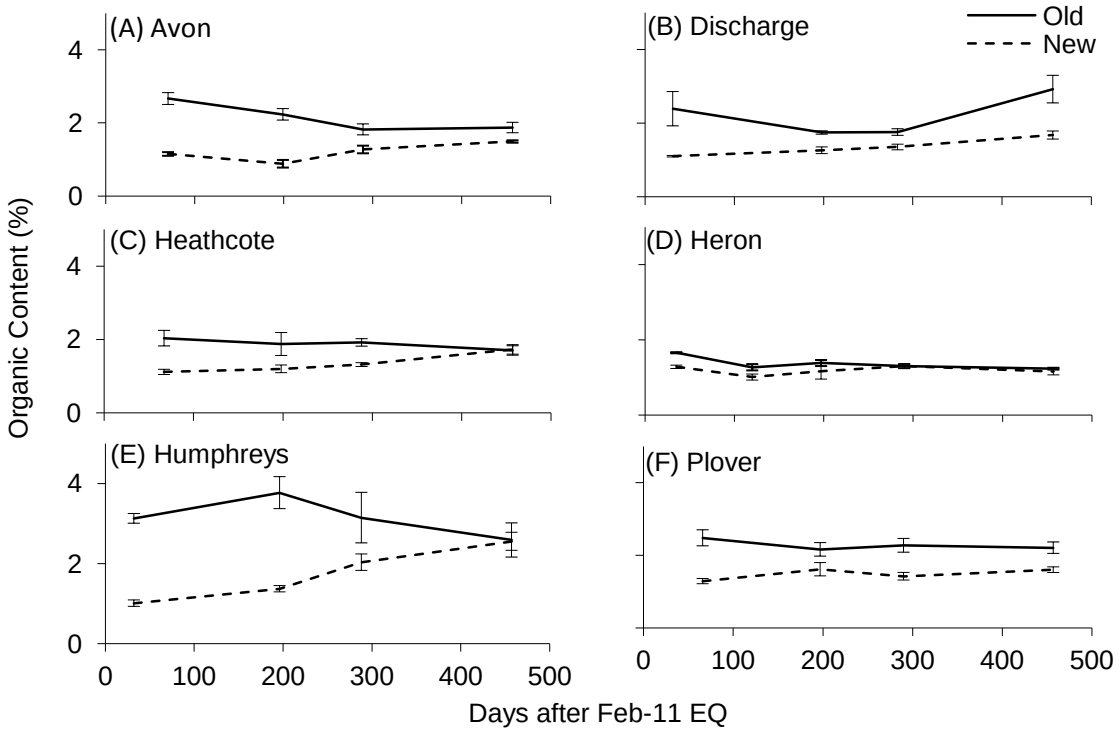

Figure 3.9. Average organic content (±SE) of surface (<2cm depth) sediments produced by the February 2011 earthquake at six sites (Avon (A), Discharge (B), Heathcote (C), Heron (D), Humphreys (E) and Plover (F)) over dates from February 2011 to May 2012. N=5 replicates per sediment type per sampling date per site.

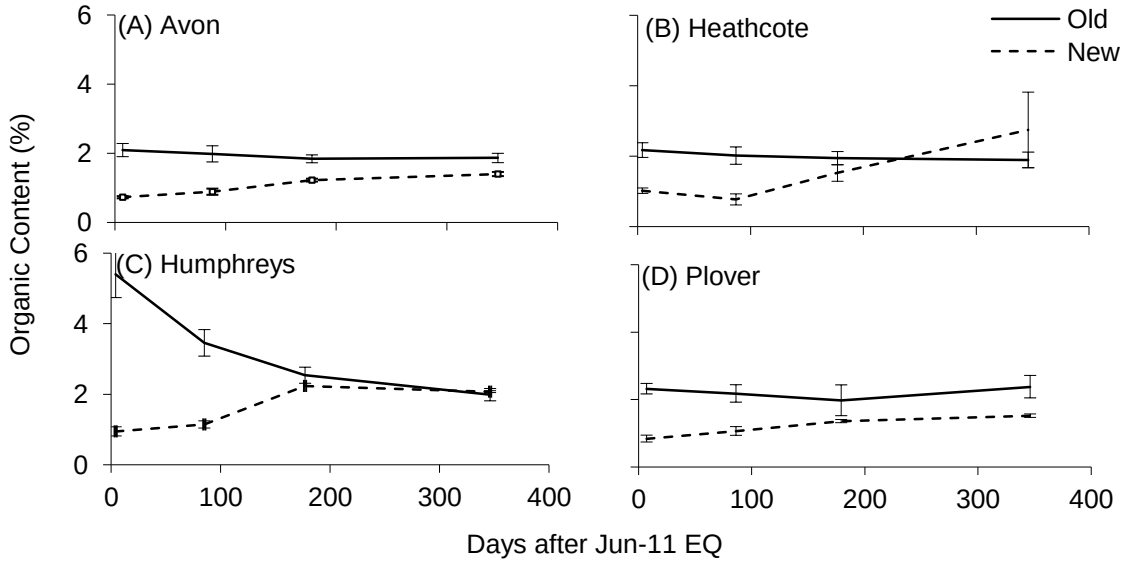

Figure 3.10. Average organic content (±SE) of surface (<2cm depth) sediments produced by the June 2011 earthquake at four sites (Avon (A), Heathcote (B), Humphreys (C) and Plover (D)) over four sampling dates from June 2011 to May 2012. N=5 replicates per sediment type per sampling date per site.

Table 3.3. General linear model showing the organic content of sediments taken from vertical cores collected from old and new sediments at six sites (Avon, Discharge, Heathcote, Heron, Humphreys and Plover) over three sampling dates (April 2011, July 2011, May 2012). Cores from old sediments were sampled at the surface, 30cm below the surface and 60cm below the surface. Cores from new sediments were sampled at the surface, the old surface (buried sediment surface), 30cm below the old surface and 60cm below the old surface. N=3 replicates per sediment type per depth per sampling date per site. Si=site, SD=sampling date, ST=sediment type. *Cochran's C still significant following log transformation so p-value reduced to 0.01.

	Surface			**Old Sed Surf vs New Sed Old Surf**			**30cm**			**60cm**		
	DF	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**
Si	5	2.78	0.14	5	28.24	**0.0011**	5	5.09	0.049*	5	7.40	**0.023**
SD	1	0.00	0.97	1	0.00	0.98	1	0.65	0.47	1	5.28	0.094
ST	1	11.01	0.19	1	1.02	0.50	1	1.75	0.41	1	0.0015	0.98
Si*SD	5	0.92	0.53	5	0.92	0.53	5	5.71	0.039*	5	3.73	0.087
Si*ST	5	7.06	**0.026**	5	2.62	0.16	5	2.59	0.16	5	3.35	0.11
SD*ST	1	11.51	**0.019**	1	14.14	0.013*	1	0.19	0.68	1	0.75	0.43
Si*SD*ST	5	1.37	0.25	5	0.71	0.62	5	0.48	0.79	5	0.62	0.68

There were some interesting differences in the grain size composition of old and new sediments. Analyses were done to examine whether the proportion of sediment particles in each grain size class varied among sites, between the initial and final sampling dates, and between old and new sediments. The outputs (Table 3.4) show there were no significant effects of site, sampling date or sediment type on the proportion of sediments sized <63µm (silt) over the study period. However, the proportion of sediments sized from 63-125µm (very fine sand) differed significantly across sites for both data sets and there was a significant site x sampling date x sediment type interaction effect for the February 2011 earthquake data set. For new sediments produced by the February 2011 earthquake, there were significant differences in the proportion of coarser sediments (125-250µm (fine sand) and 250-500µm (coarse sand)) among sites. For new sediments produced by the June 2011 earthquake, there was a significant site x sampling date x sediment type interaction for the 125-250µm grain size class, and a significant sediment type x sampling date interaction effect occurred for sediments sized from 250-500µm (Table 3.4). During the first sampling date after both the February 2011 and June 2011 earthquakes, the surface of the new sediments, produced by each earthquake, were coarser than the surface of the surrounding old sediments, although the magnitude of this difference varied by site (Figs. 3.12 and 3.13). At all sites, except Humphreys and Heathcote, both old and new sediments were dominated by sediment grains sized from 125-250µm, but old sediments had higher proportions of sediment sized <63µm (i.e., they were muddier). This caused the texture of the new sediment to be 'firm' whereas the old sediments were often 'mucky.' For example, new sediments could easily be

walked on whereas walkers sunk into the old sediments. Discharge and Humphreys had the finest (muddiest) old sediments whereas Heron and Plover were coarser, dominated by sediments of a larger grain size.

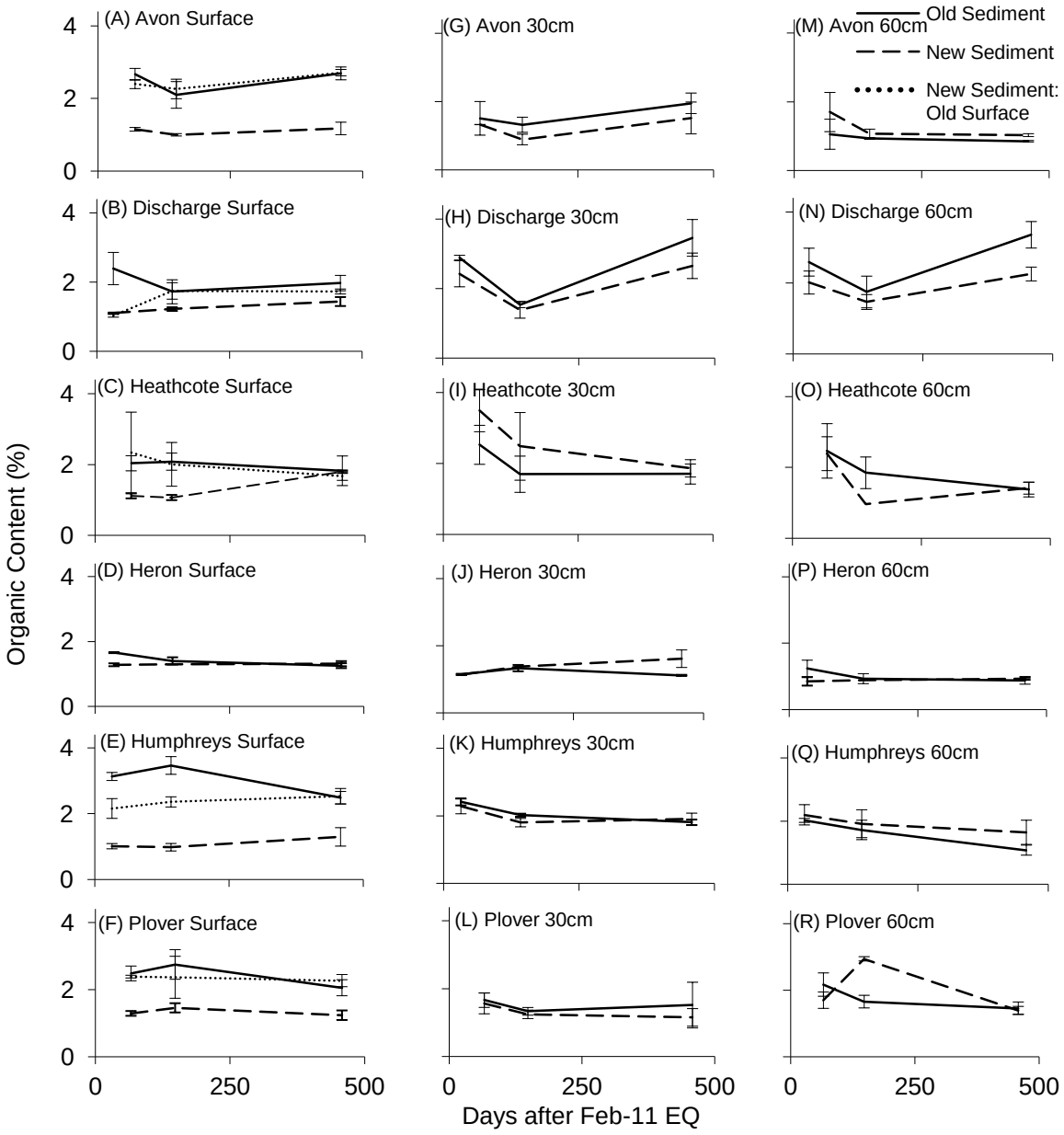

Figure 3.11. Average (±SE) organic content of sediment from old and new sediments produced by the February 2011 earthquake at six sites (Avon (A,G,M), Discharge (B,H,N), Heathcote (C,I,O), Heron (D,J,P), Humphreys (E,K,Q) and Plover (F,L,)) over three sampling dates. Old sediment samples were collected at three depths (surface, 30cm below surface and 60cm below surface) and new sediment samples collected at four depths (new surface (i.e., new sediments from earthquake), old surface (i.e., sediment surface prior to the earthquake), 30cm below the old surface and 60cm below the old surface. N=3 replicates per sediment type per sampling date per site.

For the vertical sediment cores, the grain size of the surface of the old sediments and the old surface under the new sediments was not significantly

different across sites (Table 3.5). There was considerable variability in the grain sizes of the surface sediments among sites (Figs. 3.14-3.19), and patterns were similar to those previously discussed for both old and new sediments. In general, the grain size of sediments at 30cm and 60cm were similar between old and new sediments within each site but again, there was site variation. This is to be expected due to the penetration to old sediments at these depths in both sediment types. At Plover and Heron, sediments at 30 and 60cm had a similar grain size distribution whereas at Heathcote and Discharge there was much more variability between these depths. At Heron and Plover, sediments sized from 125-250µm dominated the sediment composition at all depths. This was also generally the case at Avon but at Heathcote, Discharge and especially Humphreys, there was a higher proportion of finer grained sediments. At these latter sites, there was a trend of the sediments at 60cm to be coarser relative to sediments at 30cm within old or new sediments within a site.

Table 3.4. General linear model analysis showing differences in the grain size of surface sediments from six sites (Avon, Discharge, Heathcote, Heron, Humphreys, Plover) over two sampling dates (April 2011 and May 2012) and across two sediment types (old and new) after the February 2011 (A) and June 2011 (B) earthquakes. Each grain size fraction has been analysed independently. N=5 replicates per sediment type per sampling date per site. Si=site, ST=sediment type, SD=sampling date.

(A) Post-Feb-11 EQ

	<63µm			63-125µm			125-250µm			250-500µm		
	DF	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**
Si	5	1.01	0.49	5	26.98	**0.0013**	5	36.45	**<0.001**	5	91.27	**<0.001**
ST	1	2.68	0.35	1	4.96	0.27	1	4.79	0.27	1	3.84	0.30
SD	1	2.33	0.48	1	7.36	0.61	1	0.78	0.61	1	0.01	0.94
Si*ST	5	1.06	0.48	5	1.49	0.34	5	1.61	0.31	5	2.68	0.15
Si*SD	5	1.05	0.48	5	0.55	0.74	5	0.30	0.89	5	0.22	0.94
ST*SD	1	0.63	0.46	1	0.93	0.38	1	3.24	0.13	1	5.59	0.064
Si*ST*SD	5	0.52	0.76	5	2.36	**0.049**	5	2.13	0.072	5	1.15	0.34

(B) Post-Jun-11 EQ

	<63µm			63-125µm			125-250µm			250-500µm		
	DF	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**
Si	3	0.96	0.51	3	270.85	**<0.001**	3	6.21	0.084	3	35.10	**0.0078**
ST	1	0.35	0.66	1	16.60	0.15	1	2.90	0.34	1	11.05	0.19
SD	1	0.87	0.57	1	5.67	0.63	1	0.47	0.64	1	1.11	0.45
Si*ST	3	1.05	0.49	3	5.33	0.10	3	0.59	0.66	3	3.05	0.19
Si*SD	3	0.98	0.51	3	0.20	0.89	3	0.69	0.62	3	2.32	0.25
ST*SD	1	1.17	0.35	1	1.45	0.31	1	3.12	0.17	1	7.91	0.050
Si*ST*SD	3	0.72	0.55	3	1.08	0.36	3	8.61	**<0.001**	3	0.38	0.77

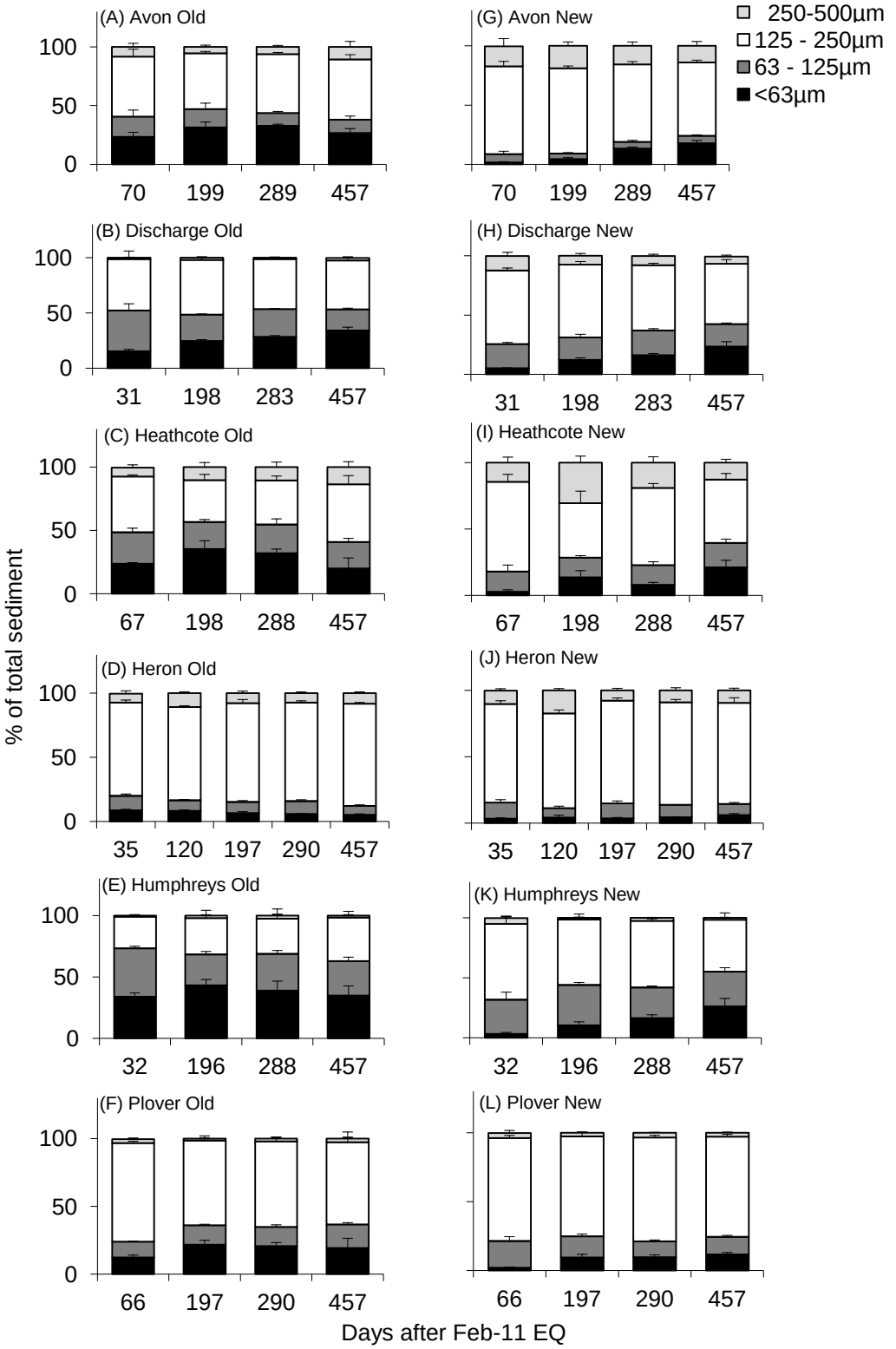

Figure 3.12. Average (+SE) grain size of old (A-F) and new (G-L) sediments produced by the February 2011 earthquake at six sites (Avon (A,G), Discharge (B,H), Heathcote (C,I), Heron (D,J), Humphreys (E,K) and Plover (F,L)) over sampling dates from February 2011 to May 2012. N=5 replicates per sediment type per sampling date per site.

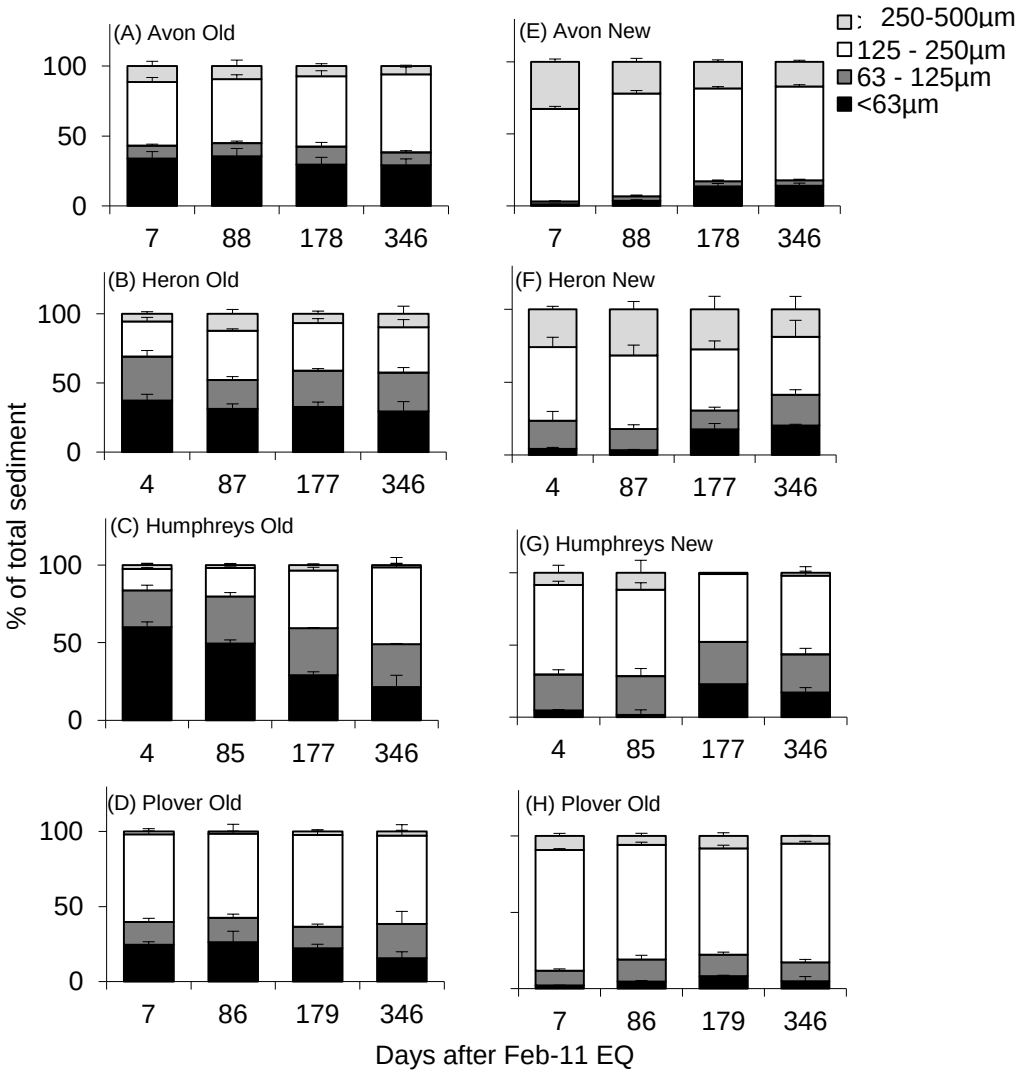

Figure 3.13. Average (+SE) grain size of old (A-D) and new (E-H) sediments produced by the June 2011 earthquake at four sites (Avon (A,E), Heathcote (B,F), Humphreys (C,G) and Plover (D,H)) over sampling dates from June 2011 to May 2012. N=5 replicates per sediment type per sampling date per site.

Table 3.5. General linear model analysis showing differences in the grain size of sediments taken from vertical long cores at three (old sediments) or four (new sediments) depths. Old sediment samples were collected at three depths (surface and 30/60cm below the surface) and new sediment samples collected at four depths (new surface (i.e., new sediments from EQ), old surface (sediment surface prior to the earthquake), and 30/60cm below the old surface. Samples were collected from six sites (Avon, Discharge, Heathcote, Heron, Humphreys, Plover) and analysed over two sampling dates (initial and final) after the February 2011 (A) and June 2011 (B) earthquakes. Each grain size fraction has been analysed independently. Si=site, SD=sampling date, ST=sediment type. N=5 replicates per sediment type per depth per sampling date per site. *Cochran's C still significant following log transformation so p-value reduced to 0.01.

(A) Surface

	<63µm			63-125µm			125-250µm			250-500µm		
	DF	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**
Si	5	2.35	0.18	5	5.69	0.040*	5	5.17	0.048*	5	2.14	0.21
ST	1	4.65	0.28	1	33.68	0.11	1	6044.03	**0.0082**	1	104.41	0.062
SD	1	1.69	0.39	1	4.07	0.24	1	5.13	0.29	1	0.75	0.46
Si*ST	5	7.84	0.021*	5	2.34	0.19	5	3.32	0.11	5	3.67	0.090
Si*SD	5	4.33	0.067	5	2.00	0.23	5	1.91	0.25	5	3.02	0.13
ST*SD	1	34.53	**0.002**	1	0.19	0.68	1	0.004	0.95	1	0.36	0.58
Si*ST*SD	5	1.25	0.30	5	1.81	0.13	5	3.43	**0.010**	5	1.53	0.20

(B) Old sediment surface versus new sediment old surface

	<63µm			63-125µm			125-250µm			250-500µm		
	DF	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**
Si	5	10.36	0.011*	5	6.66	0.029*	5	6.78	0.028*	5	7.03	**0.026**
ST	1	0.45	0.62	1	6.54	0.24	1	0.20	0.73	1	14.86	0.16
SD	1	2.34	0.37	1	3.79	0.14	1	2.55	0.26	1	0.023	0.89
Si*ST	5	0.58	0.72	5	0.49	0.77	5	0.72	0.64	5	5.02	0.051
Si*SD	5	0.99	0.51	5	4.86	0.054	5	2.60	0.16	5	5.81	**0.038**
ST*SD	1	4.40	0.090	1	0.12	0.74	1	0.084	0.78	1	0.67	0.45
Si*ST*SD	5	3.76	**0.0066**	5	0.88	0.50	5	1.99	0.099	5	0.56	0.73

(C) 30cm

	<63µm			63-125µm			125-250µm			250-500µm		
	DF	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**
Si	5	6.40	0.031*	5	5.05	0.050	5	3.92	0.080	5	3.40	0.10
ST	1	1.92	0.40	1	0.0086	0.94	1	6.47	0.24	1	2.05	0.39
SD	1	1.55	0.28	1	5.53	0.095	1	1.10	0.34	1	0.14	0.73
Si*ST	5	6.31	0.032*	5	1.86	0.26	5	2.10	0.22	5	0.67	0.67
Si*SD	5	6.96	0.026*	5	3.69	0.089	5	31.08	**<0.001**	5	6.64	**0.029**
ST*SD	1	0.27	0.63	1	0.48	0.52	1	0.14	0.73	1	0.70	0.44
Si*ST*SD	5	0.88	0.50	5	1.56	0.19	5	0.50	0.78	5	0.93	0.47

(D) 60cm

	<63µm			63-125µm			125-250µm			250-500µm		
	DF	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**
Si	5	7.95	**0.020**	5	10.07	**0.012**	5	6.14	0.034*	5	3.33	0.11
ST	1	0.25	0.71	1	0.27	0.69	1	5.83	0.25	1	6199.16	**0.0081**
SD	1	0.52	0.50	1	36.82	0.85	1	0.95	0.46	1	1.68	0.34
Si*ST	5	4.21	0.070	5	1.21	0.42	5	1.48	0.34	5	1.28	0.40
Si*SD	5	8.53	**0.017**	5	1.00	0.50	5	2.08	0.22	5	2.74	0.15
ST*SD	1	3.17	0.13	1	0.13	0.73	1	0.21	0.66	1	0.000	0.98
Si*ST*SD	5	0.69	0.63	5	1.91	0.11	5	1.67	0.16	5	1.77	0.14

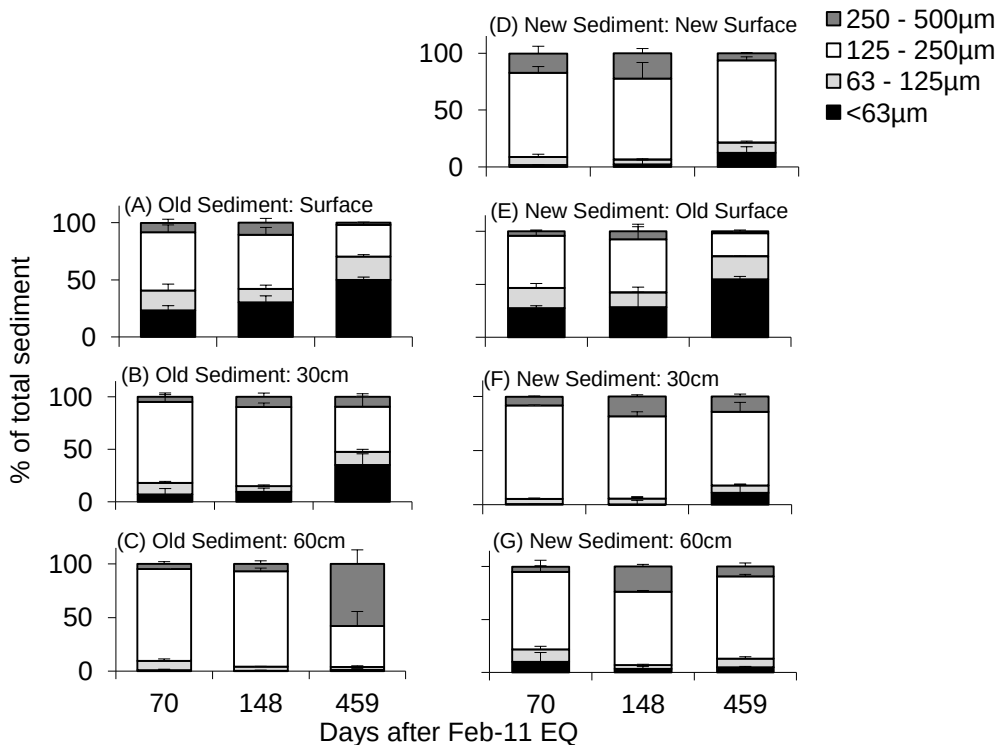

Figure 3.14. Average (+SE) vertical grain size distribution of old (A-C) and new (D-G) sediments produced by the February 2011 earthquake at **Avon.** Old sediments were collected at three depths (surface (A), 30cm (B) and 60cm (C) below the surface) and new sediment samples collected at four depths (new surface (i.e., new sediments from EQ) (D), old surface (sediment surface prior to the earthquake) (E), 30cm (F) and 60cm (G) below the old surface. N=3 replicates per sediment type per depth per sampling date per site.

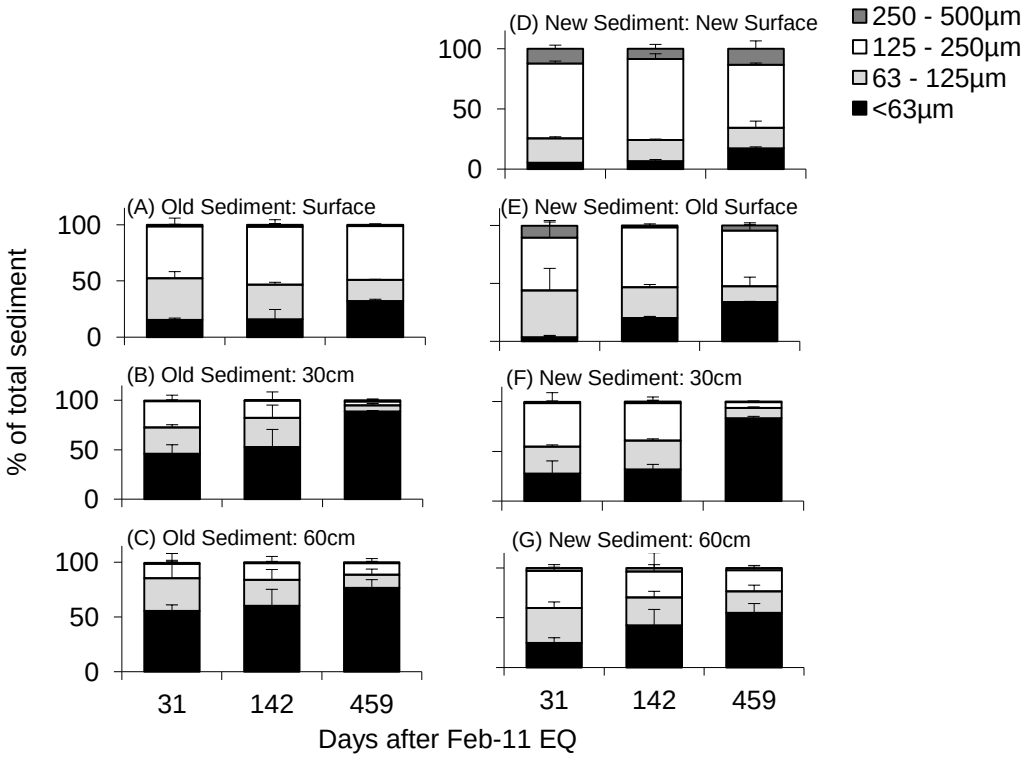

Figure 3.15. Average (+SE) vertical grain size distribution of old (A-C) and new (D-G) sediments produced by the February 2011 earthquake at **Discharge.** Old sediments were collected at three depths (surface (A), 30cm (B) and 60cm (C) below the surface) and new sediment samples collected at four depths (new surface (i.e., new sediments from EQ) (D), old surface (sediment surface prior to the earthquake) (E), 30cm (F) and 60cm (G) below the old surface. N=3 replicates per sediment type per depth per sampling date per site.

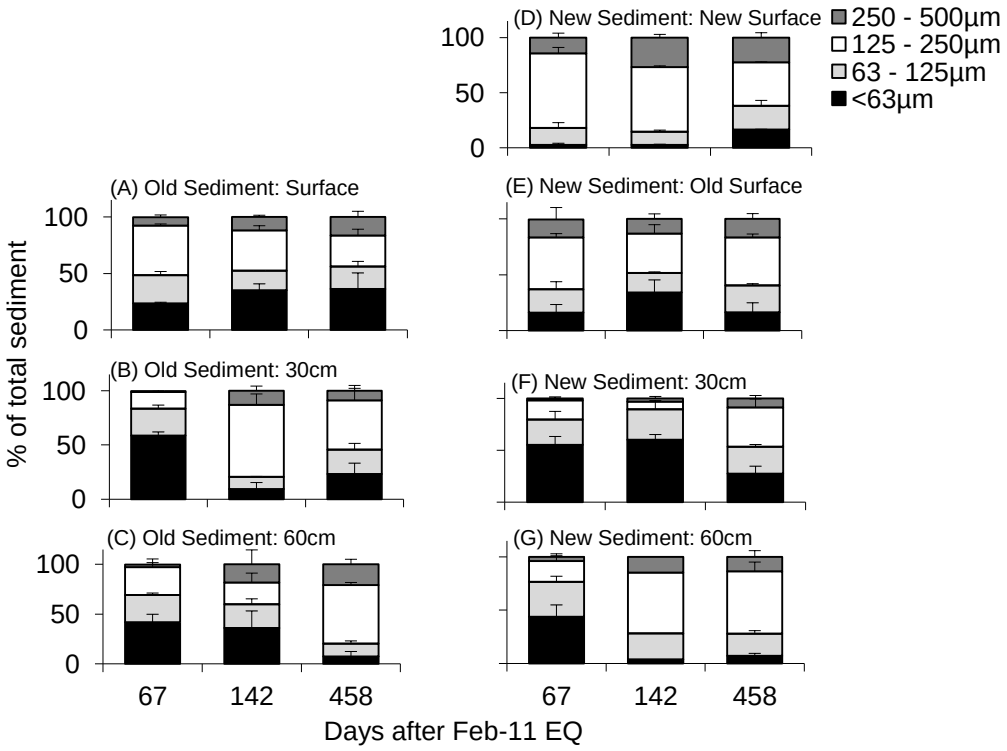

Figure 3.16. Average (+SE) vertical grain size distribution of old (A-C) and new (D-G) sediments produced by the February 2011 earthquake at **Heathcote.** Old sediments were collected at three depths (surface (A), 30cm (B) and 60cm (C) below the surface) and new sediment samples collected at four depths (new surface (i.e., new sediments from EQ) (D), old surface (sediment surface prior to the earthquake) (E), 30cm (F) and 60cm (G) below the old surface. N=3 replicates per sediment type per depth per sampling date per site.

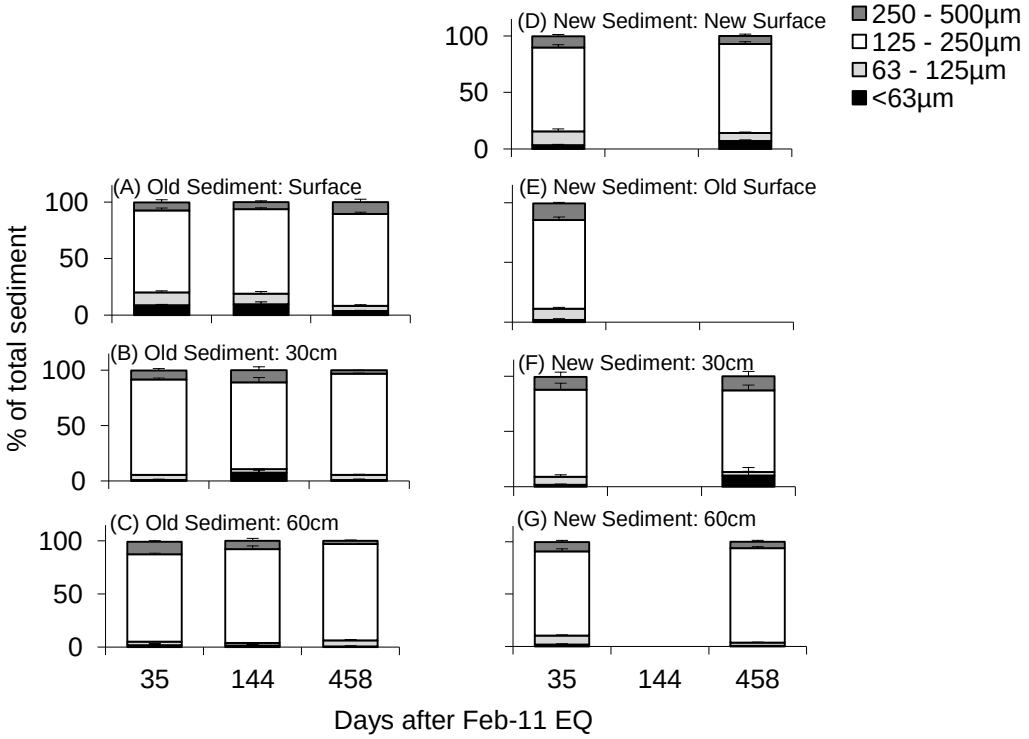

Figure 3.17. Average (+SE) vertical grain size distribution of old (A-C) and new (D-G) sediments produced by the February 2011 earthquake at **Heron.** Old sediments were collected at three depths (surface (A), 30cm (B) and 60cm (C) below the surface) and new sediment samples collected at four depths (new surface (i.e., new sediments from EQ) (D), old surface (sediment surface prior to the earthquake) (E), 30cm (F) and 60cm (G) below the old surface. N=3 replicates per sediment type per depth per sampling date per site.

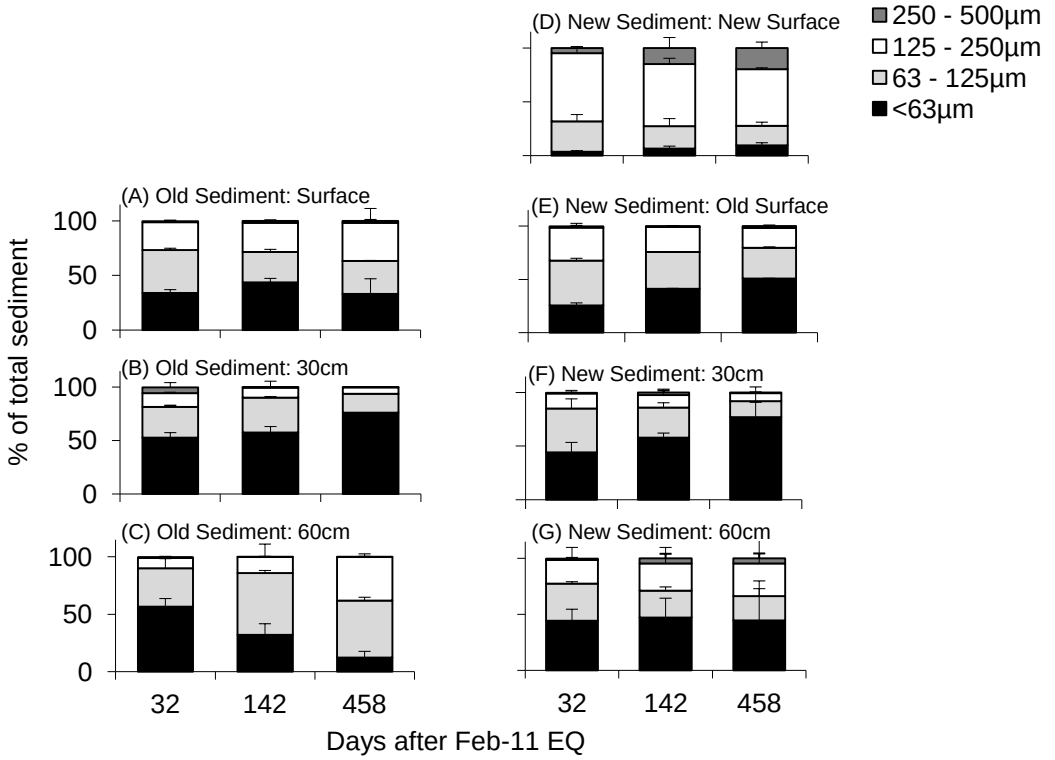

Figure 3.18. Average (+SE) vertical grain size distribution of old (A-C) and new (D-G) sediments produced by the February 2011 earthquake at **Humphreys.** Old sediments were collected at three depths (surface (A), 30cm (B) and 60cm (C) below the surface) and new sediment samples collected at four depths (new surface (i.e., new sediments from EQ) (D), old surface (sediment surface prior to the earthquake) (E), 30cm (F) and 60cm (G) below the old surface. N=3 replicates per sediment type per depth per sampling date per site.

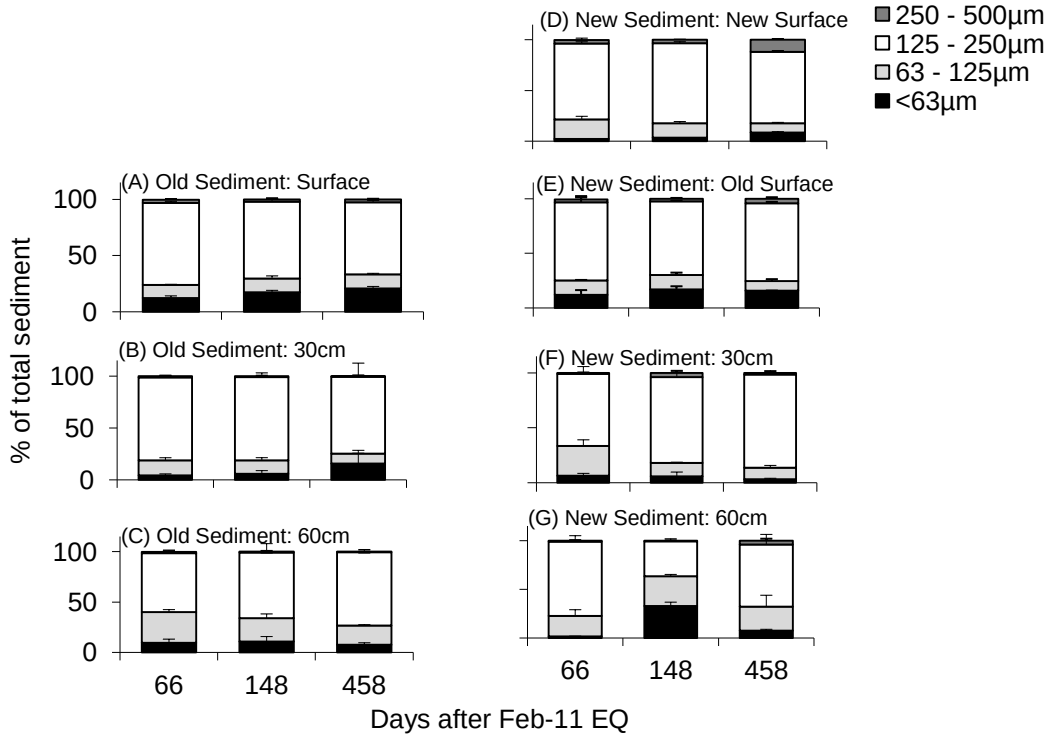

Figure 3.19. Average (+SE) vertical grain size distribution of old (A-C) and new (D-G) sediments produced by the February 2011 earthquake at **Plover.** Old sediments were collected at three depths (surface (A), 30cm (B) and 60cm (C) below the surface) and new sediment samples collected at four depths (new surface (i.e., new sediments from EQ) (D), old surface (sediment surface prior to the earthquake) (E), 30cm (F) and 60cm (G) below the old surface. N=3 replicates per sediment type per depth per sampling date per site.

3.3.3. Marine plant percentage cover

For new sediments produced by the February 2011 earthquake, there were significant effects of site, sampling date, sediment type and quadrat(site) (all $p<0.001$) on the percentage cover of marine plant community composition. The site x sampling date x sediment type interaction effect was significant (Pseudo-$F_{68,236}=4.01$ $p<0.001$) (Table 3.6A). With the exception of Heron, there was generally a greater percentage cover of benthic microalgae (BMA) on new sediments than old sediments across the sampling dates (Fig. 3.20). At Humphreys, there was an increase in the percentage cover of BMA over time and the percentage cover in old and new sediments were similar by the final sampling date. At Heathcote, new sediments showed a reduction in the percentage cover of BMA over the sampling dates. The percentage cover of *Gracilaria chilensis* was highest at Discharge, Heathcote and Humphreys where there was greater cover in old versus new sediments. In old sediments at Humphreys, there was a clear reduction in the percentage cover of *Gracilaria* over time whereas at Discharge, the percentage cover of *Gracilaria* on old and new sediments showed a general increasing trend. *Ulva* spp. occurred at all sites except Avon and was generally more abundant in old than new sediments. The percentage cover of *Ulva* peaked in December 2011 (summer) across these sites. *Zostera muelleri* occurred only in old sediments at Plover and Heron.

For new sediments produced by the June 2011 earthquake, there were significant effects of sampling date and site x sampling date on the percentage cover of marine plant community composition. The sediment type x quadrat(site) interaction effect was also significant (Table 3.6B). This data set showed there to be a similar percentage cover of BMA in old and new sediments within sites, with the exception of Plover, where BMA did not occur on new sediments (Fig. 3.21). The percentage cover of BMA peaked in December 2011 across all sites. The percentage cover of *Gracilaria* was fairly low among sites, with similar levels of cover occurring between old and new sediments within sites. Following peaks in September 2011 (Heathcote, Humphreys, Plover) and December 2011 (Avon), *Gracilaria* disappeared from all sites. *Ulva* occurred only, above negligible levels, at Humphreys, where there was similar coverage on old and new sediments. *Zostera* was absent from all sites except Plover where it occurred in old and new sediments from December 2011.

Table 3.6. PERMANOVA analyses for surface (<2cm depth) fauna and marine plant percentage cover for old and new sediments sampled after the February 2011 (A) and June 2011 (B) earthquakes. For (A), site = fixed factor with six levels (Avon, Discharge, Heathcote, Heron, Humphreys, Plover); sediment type = fixed factor with two levels (old and new); sampling date = random factor with four levels (April/May 2011, September 2011, December 2011, May 2012); quadrat = random factor with five levels (replicates) nested within site. For (B), site = fixed factor with four levels (Avon, Heathcote, Humphreys and Plover), sediment type =fixed factor with two levels (old and new); sampling date = random factor with four levels (June 2011, September 2011, December 2011, May 2012); quadrat = random factor with five levels (replicates) nested within site. N=5 replicates per sediment type per sampling date per site.

(A) Feb-11 EQ

	Surface Fauna			Marine Plant % Cover		
	DF	**Pseudo-F**	**p**	**DF**	**Pseudo-F**	**p**
Site (Si)	5	10.01	**<0.001**	5	5.27	**<0.001**
Sampling Date (SD)	3	26.80	**<0.001**	3	12.36	**<0.001**
Sediment Type (ST)	1	3.68	**0.036**	1	6.35	**0.0013**
Replicate (Re) nested in Si	24	1.53	**0.015**	24	1.83	**0.0043**
Si*SD	15	5.28	**<0.001**	15	9.62	**<0.001**
Si*ST	5	2.29	**0.008**	5	3.58	**<0.001**
SD*ST	3	2.82	**0.009**	3	11.35	**<0.001**
SD*Re(Si)	71	1.00	0.49	71	1.80	0.29
ST*Re (Si)	24	1.10	0.32	24	1.43	**0.047**
Si*SD*ST	15	2.42	**<0.001**	15	3.84	**<0.001**

(B) Jun-11 EQ

	Surface Fauna			Marine Plant % Cover		
	DF	**Pseudo-F**	**p**	**DF**	**Pseudo-F**	**p**
Site (Si)	3	4.95	**<0.001**	3	1.75	0.14
Sediment Type (ST)	1	1.14	0.35	1	1.96	0.23
Sampling Date (SD)	3	19.31	**<0.001**	3	10.37	**<0.001**
Replicate (Re) nested in Si	16	1.16	0.28	16	0.83	0.72
Si*ST	3	2.03	**0.010**	3	0.96	0.49
Si*SD	9	11.19	**<0.001**	9	3.67	**<0.001**
ST*SD	3	5.81	**<0.001**	3	0.68	0.70
ST*Re(Si)	16	1.06	0.40	16	1.55	**0.047**
SD*Re (Si)	44	1.05	0.41	44	0.44	1
Si*ST*SD	9	2.45	**<0.009**	9	0.46	0.97

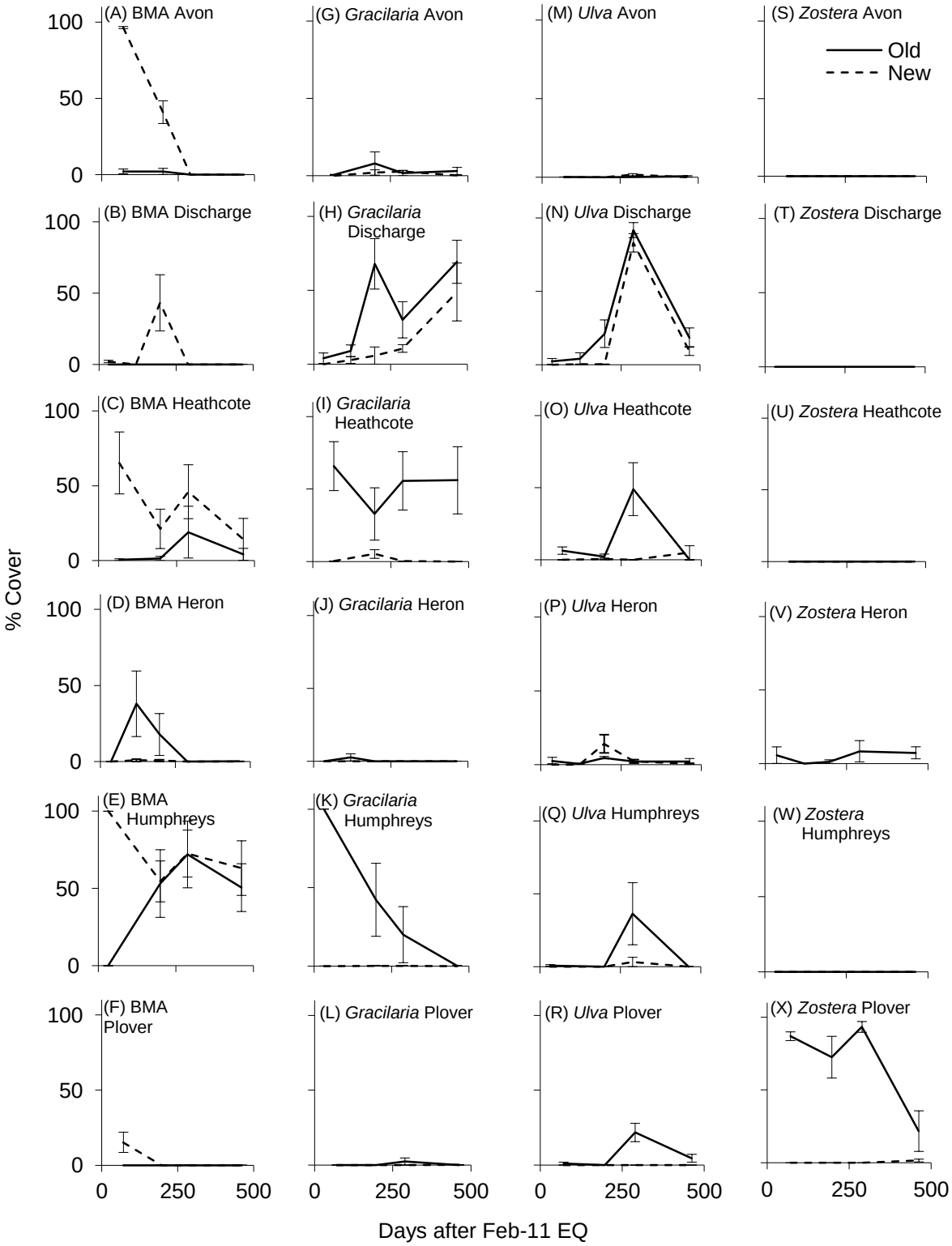

Figure 3.20. Average (±SE) percent cover of marine plants (benthic microalgae (BMA) (A-F), *Gracilaria chilensis* (G-L), *Ulva* spp. (M-R) and *Zostera muelleri* (S-X)) at six sites (Avon (A-S), Discharge (B-T), Heathcote (C-U), Heron (D-V), Humphreys (E-W) and Plover (F-X)) in areas of old and new sediment on sampling dates after the February 2011 earthquake. N=5 replicates per sediment type per sampling date per site.

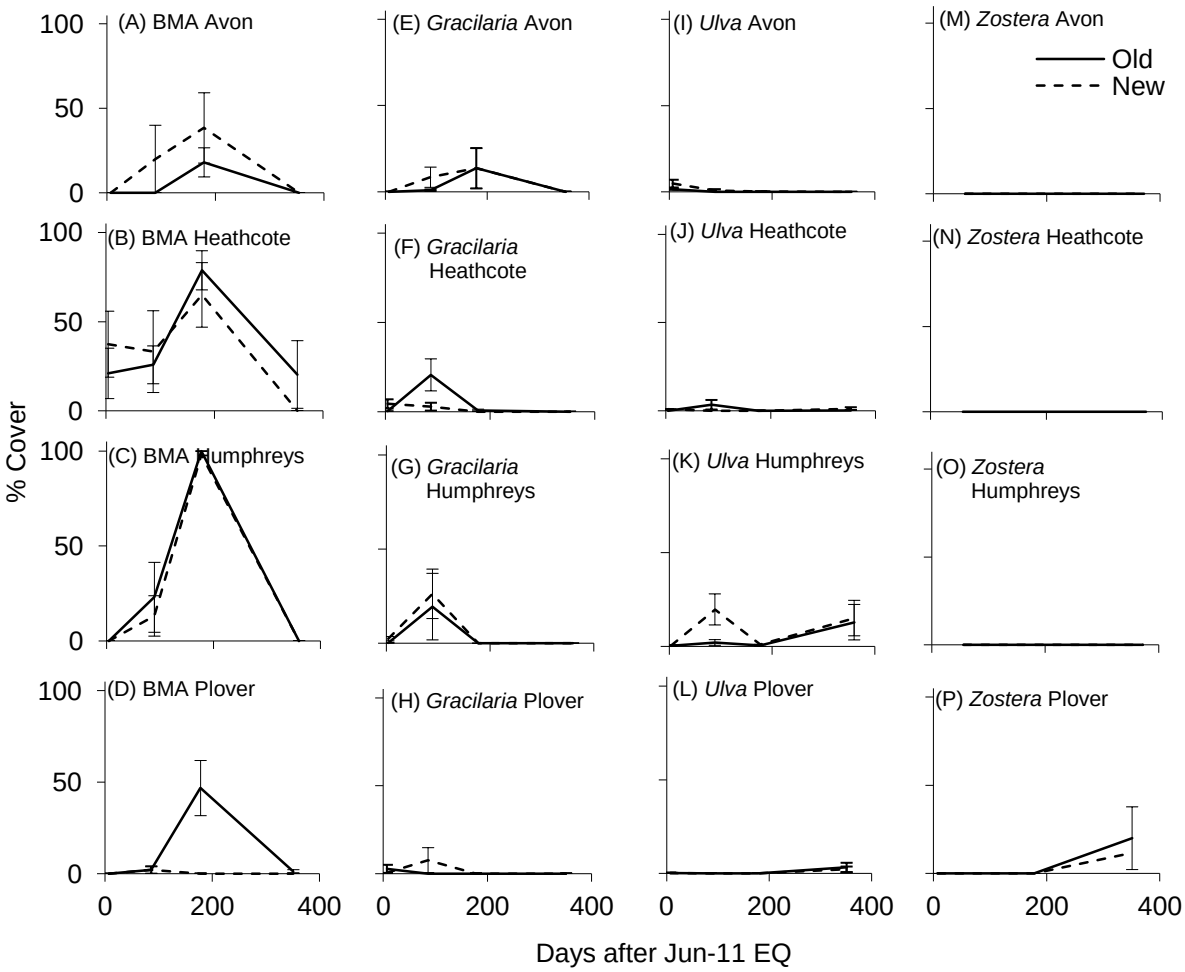

Figure 3.21. Average (±SE) percent cover of marine plants (benthic microalgae (BMA) (A-D), *Gracilaria chilensis* (E-H), *Ulva* spp. (I-L) and *Zostera muelleri* (M-P)) at four sites (Avon (A,E,I,M), Heathcote (B,F,J,N), Humphreys (C,G,K,O) and Plover (D,H,L,P)) in areas of old and new sediment on four sampling dates after the June 2011 earthquake. N=5 replicates per sediment type per sampling date per site.

3.3.4. Surface fauna

Surface faunal communities (taxa richness and number of individuals) in old and new sediments after both the February 2011 and June 2011 earthquakes differed significantly among sites and sampling dates (Table 3.6). There was a significant interaction effect of site x sediment type x sampling date for both data sets. Overall, taxa richness and the number of individuals were lowest at Humphreys and highest at Heron and Plover. Discharge and the river sites, Avon and Heathcote, generally had intermediate values and at many sites, taxa richness and the number of individuals peaked in December 2011 (Figs. 3.22 and 3.23). The number of crabs holes and, correspondingly, the predicted number of crabs (based on regression equations established in *Chapter 2* Fig. 2.9), varied temporally within sites and

between sediment types, but were generally highest at Avon and low at Humphreys, Plover and Discharge (Figs. 3.24 and 3.25).

There was a high level of dissimilarity in the community composition of surface fauna between old and new sediments within sites for sediments sampled immediately after each earthquake. This high level of dissimilarity remained over time at most sites but surface faunal communities in old and new sediments at some sites did become more similar over the 15-month (February 2011 data set) and 11-month (June 2011 data set) sampling periods. For new sediments sampled during the first sampling date after February 2011, *Amphibola crenata* was present at all sites except Heron and Humphreys, *Diloma subrostrata* and *Cominella glandiformis* occurred at Heron, and *Microlenchus tenebrosus*, *Diloma* and *Austrovenus stutchburyi* were found at Plover. For old sediments during this same initial sampling date, *Amphibola* occurred at all sites except Discharge and Humphreys, and *Macrophthalmus hirtipes* was found at Avon and Discharge. Additionally, *Cominella* were present at Discharge and Plover, *Austrovenus* at Discharge and Heron, *Diloma* at Heron, *Microenchus* at Plover, *Anthropleura* at Discharge and *Notoacmea helmsi* at Heron and Plover. By May 2012, *Austrovenus* had appeared in new sediments at Discharge, but *Amphibola* and *Macrophthalmus* were no longer present at these sites. *Amphibola* were no longer found in new sediments at Heathcote, whereas *Austrovenus*, *Amphibola* and *Microlenchus* were now present at Heron. Furthermore, no surface fauna were found in new sediments at Humphreys, and *Austrovenus* and *Amphibola* were not present at Plover. For old sediments during the final sampling date, only *Austrovenus* occurred at Discharge, *Austrovenus* was found at Heathcote (but not *Amphibola*) and there were no *Amphibola*, *Notoacmea* or *Austrovenus* at Heron.

For sediments sampled after the June 2011 earthquake, in general, differences in surface faunal community structure among sites were driven by the presence/abundance of *Microlenchus*, *Hemigrapsus*, *Diloma*, *Austrovenus* and *Eliminus* sp*.* at Avon, *Austrovenus* and *Cominella* at Heathcote, *Diloma* at Plover and the absence of any surface fauna at Humphreys. For old sediments, *Austrovenus, Cominella* and *Amphibola* were found at Heathcote, *Microlenchus* and *Austrovenus* at Avon, and *Diloma*, *Microlenchus*, *Austrovenus* and *Amphibola* at Plover. By May 2012, similar communities remained at each site, but *Amphibola*

became abundant on new sediments at Avon, and *Microlenchus* colonised new sediments at Plover.

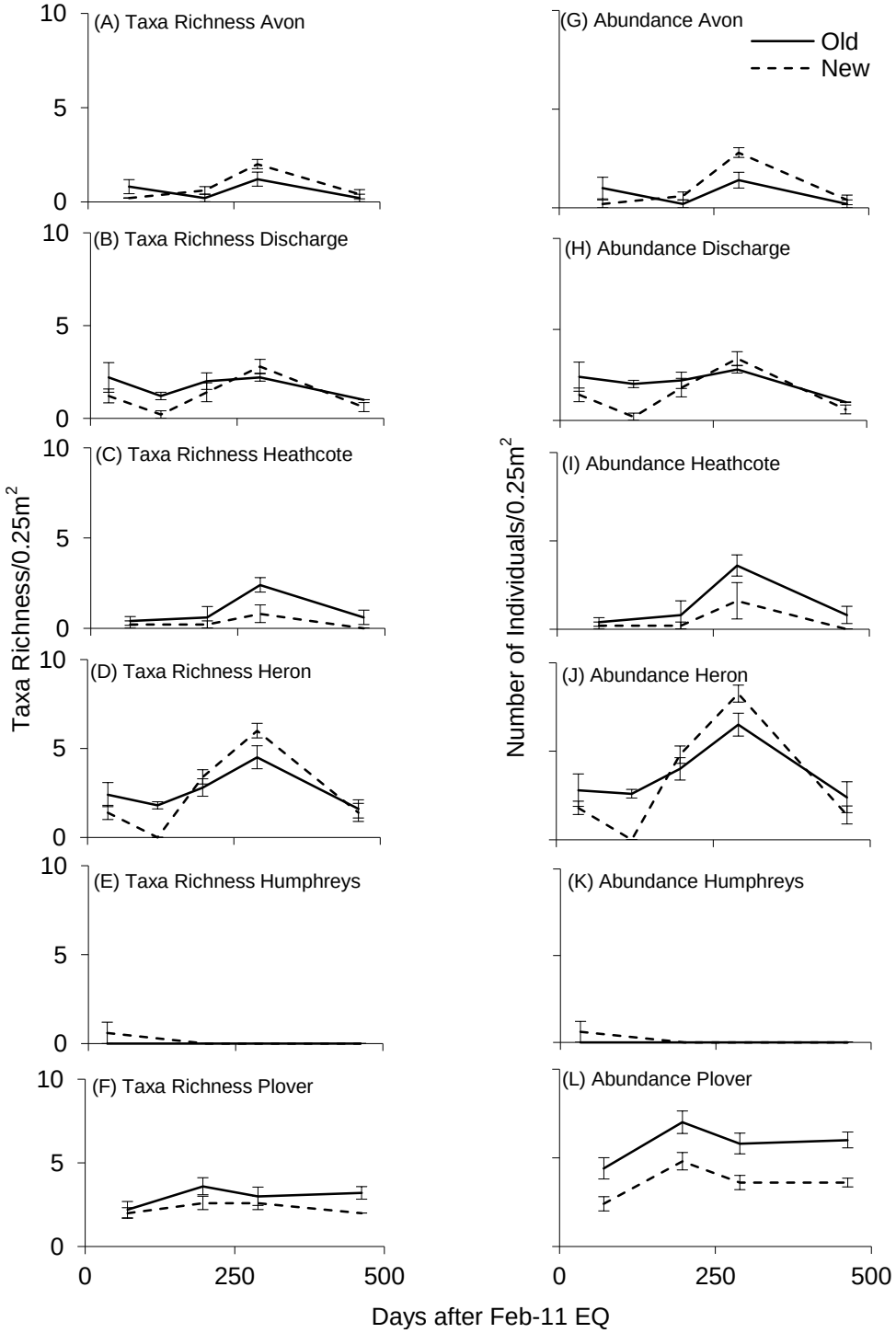

Figure 3.22. Average (±SE) taxa richness (A-F) and number of individuals (G-L) of surface (<2cm depth) fauna at six sites (Avon (A,G), Discharge (B,H), Heathcote (C,I), Heron (D,J), Humphreys (E,K) and Plover (F,L)) in areas of old and new sediment on sampling dates after the February 2011 earthquake. N=5 replicates per sediment type per sampling date per site.

PCO plots, based on distance from centroid data, showed that at most sites, surface fauna community composition in old and new sediments was more similar at the final versus the initial sampling date for both the February 2011 and June 2011 data sets (Figs. 3.26 and 3.27). Thus, the effect of sediment type diminishes over time, at least partially due to the mixing of old and new sediments.

Scatterplots of percentage mud versus taxa richness and number of individuals showed that new and old sediments form distinct clusters immediately after each earthquake event, with new sediments showing low levels of mud and old sediments showing more variable, but overall higher, levels of mud. Over time, mixing occurs as new sediments become muddier and show greater variability. In general, taxa richness increased slightly within sites over time (Figs. 3.28-3.29).

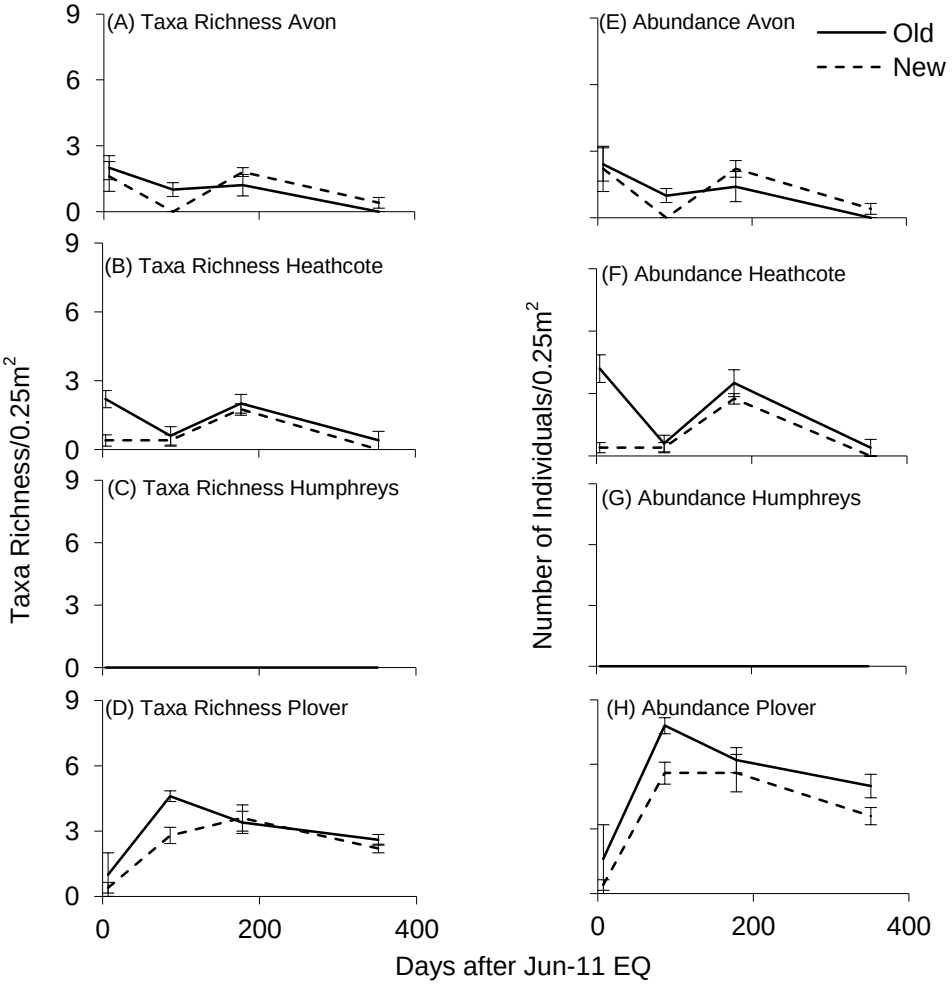

Figure 3.23. Average (±SE) taxa richness (A-D) and number of individuals (E-H) of surface (<2cm depth) fauna at four sites (Avon (A,E), Heathcote (B,F), Humphreys (C,G) and Plover (D,H)) in areas of old and new sediment on sampling dates after the June 2011 earthquake. N=5 replicates per sediment type per sampling date per site.

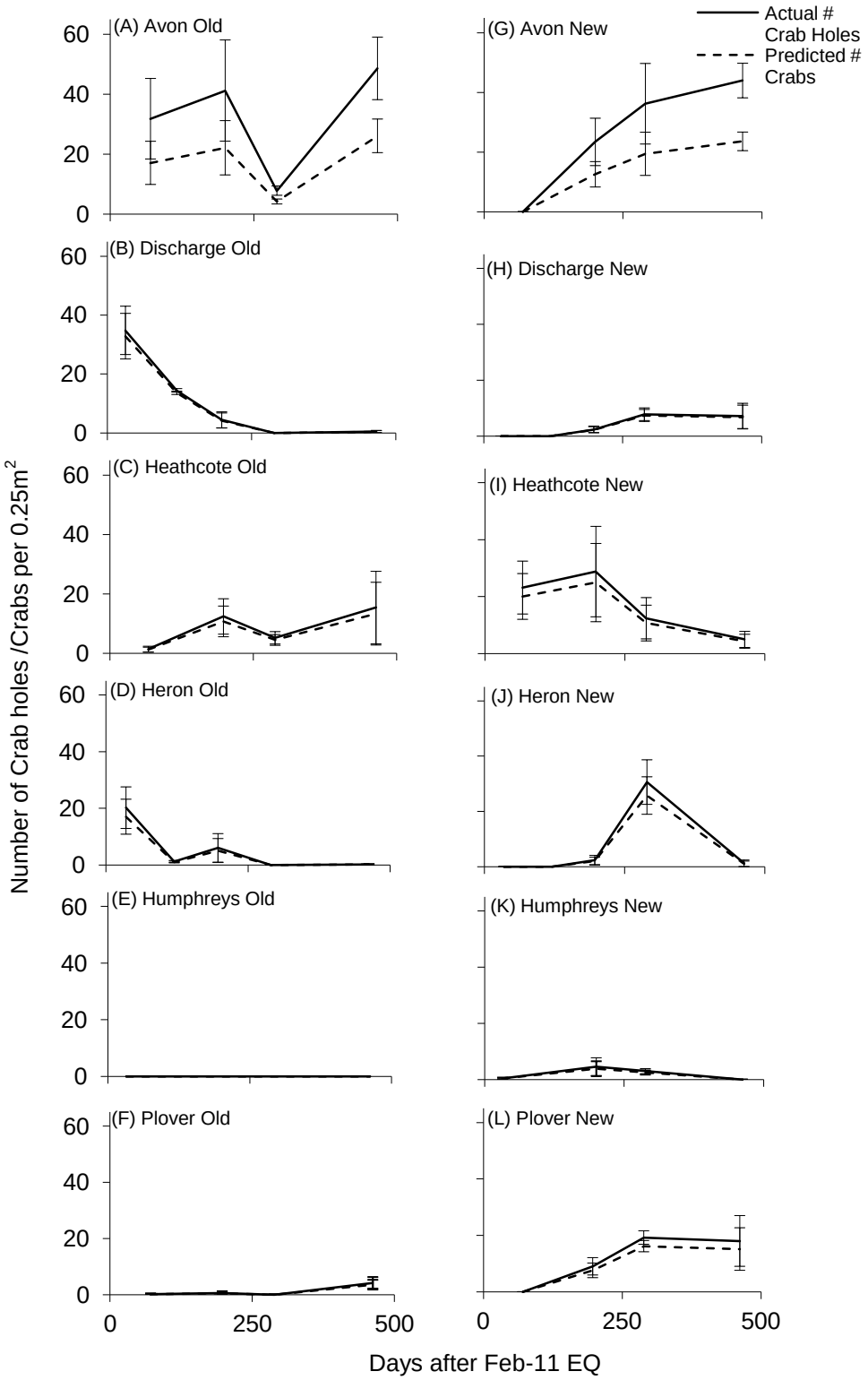

Figure 3.24. Average (±SE) actual number of crab holes and predicted number of crabs at six sites (Avon (A,G), Discharge (B,H), Heathcote (C,I), Heron (D,J), Humphreys (E,K) and Plover (F,L)) in areas of old (A-F) and new (G-L) sediment on sampling dates after the February 2011 earthquake. N=5 replicates per sediment type per sampling date per site.

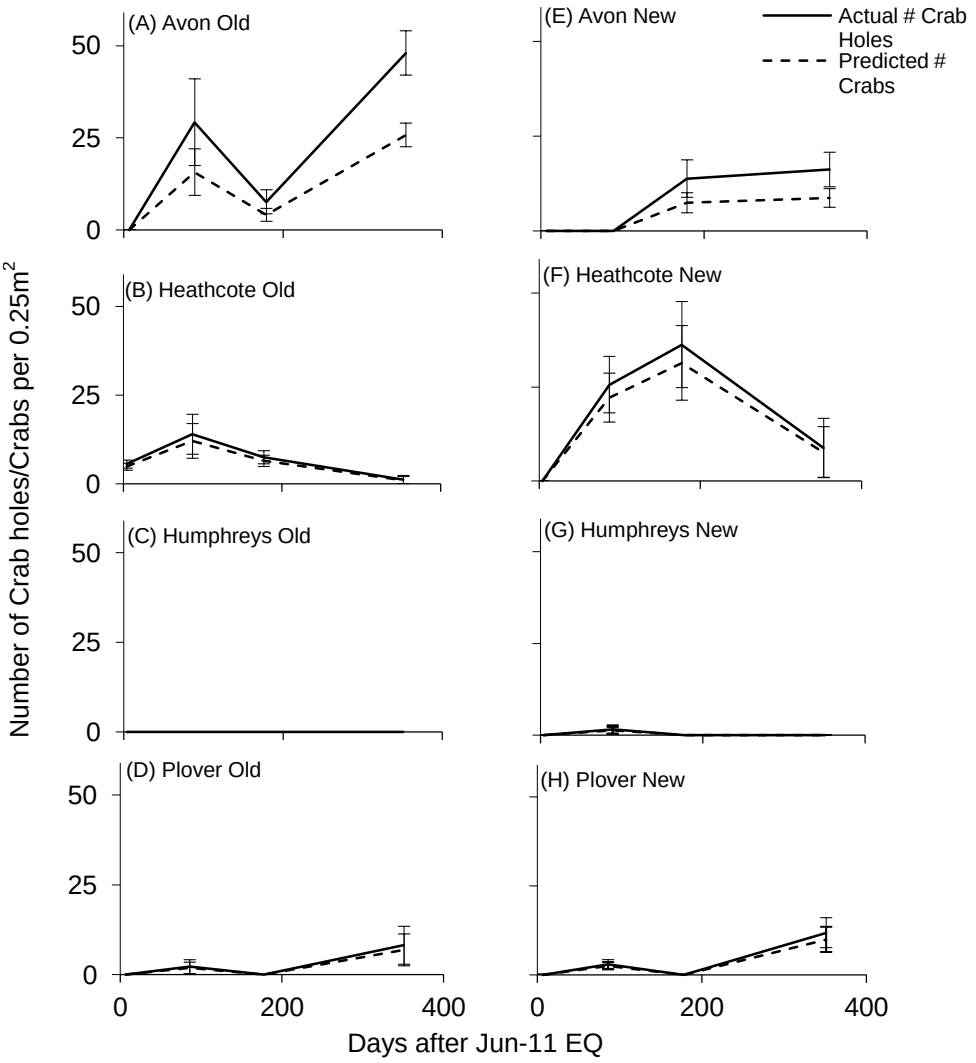

Figure 3.25. Average (±SE) actual number of crab holes and predicted number of crabs at four sites (Avon (A,E), Heathcote (B,F), Humphreys (C,G) and Plover (D,H)) in areas of old (A-D) and new (E-H) sediment on sampling dates after the June 2011 earthquake. N=5 replicates per sediment type per sampling date per site.

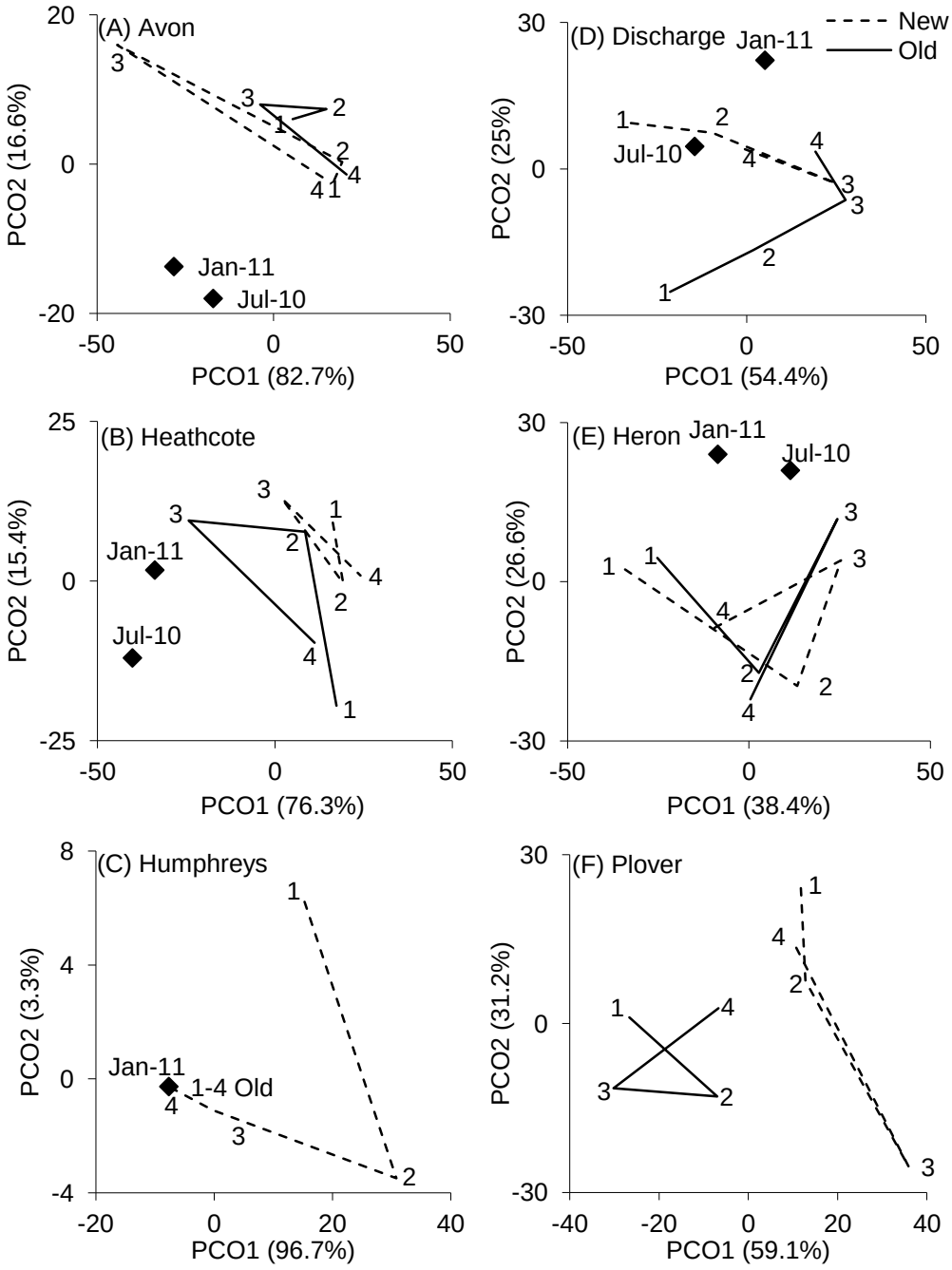

Figure 3.26. PCO plot based on distance from centroid data showing the trajectory of change of surface faunal communities over four sampling dates (1=April/May 2011, 2=September 2011, 3=December 2011, 4=May 2012) after the February 2011 earthquake at six sites (A-F). At sites where pre-earthquake data were available (taken from *Chapter 2*), the position of the community, in space, at July 2010 and January 2011 is shown. N=5. PCO1 and PCO2 values are percentage of total variation.

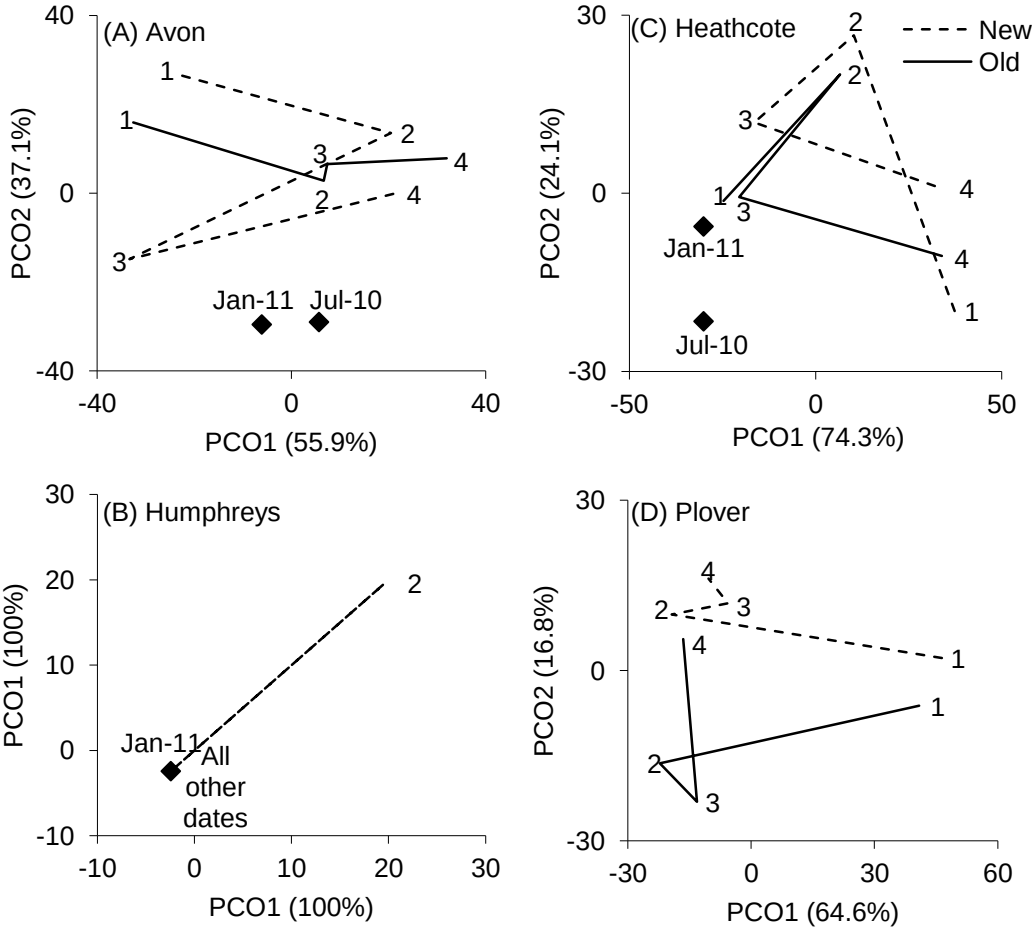

Figure 3.27. PCO plot based on distance from centroid data showing the trajectory of change of surface faunal communities over four sampling dates (1=June 2011, 2=September 2011, 3=December 2011, 4=May 2012) at four sites (A-D) after the June 2011 earthquake. At sites where pre-earthquake data were available (taken from *Chapter 2*), the position of the community, in space, at July 2010 and January 2011 is shown. N=5. PCO1 and PCO2 values are percentage of total variation.

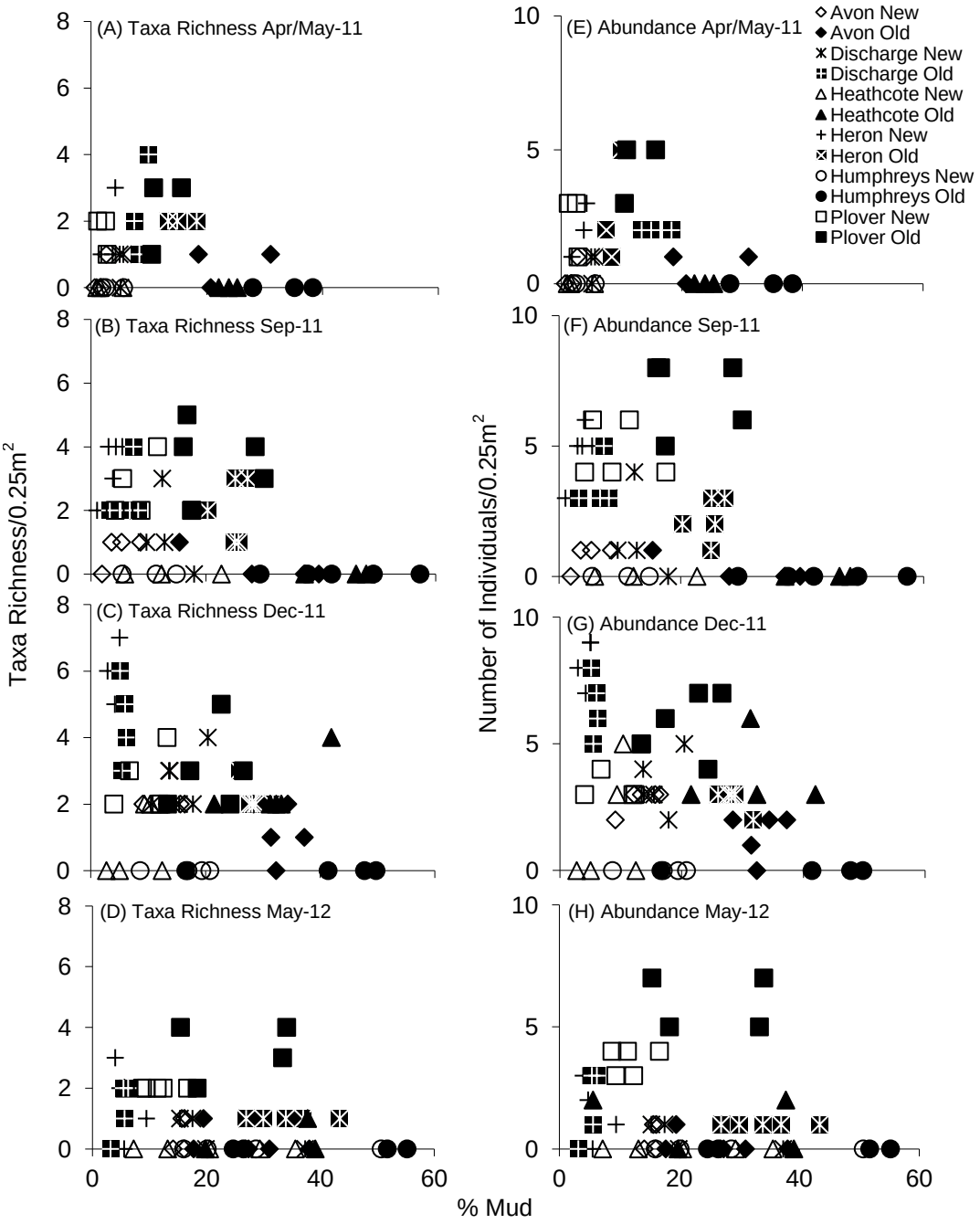

Figure 3.28. Scatterplots showing percentage mud (grain size <63µm) versus surface fauna taxa richness (A-D) and number of individuals (E-H) in old and new sediments across six sites and four sampling dates after the February 2011 earthquake.

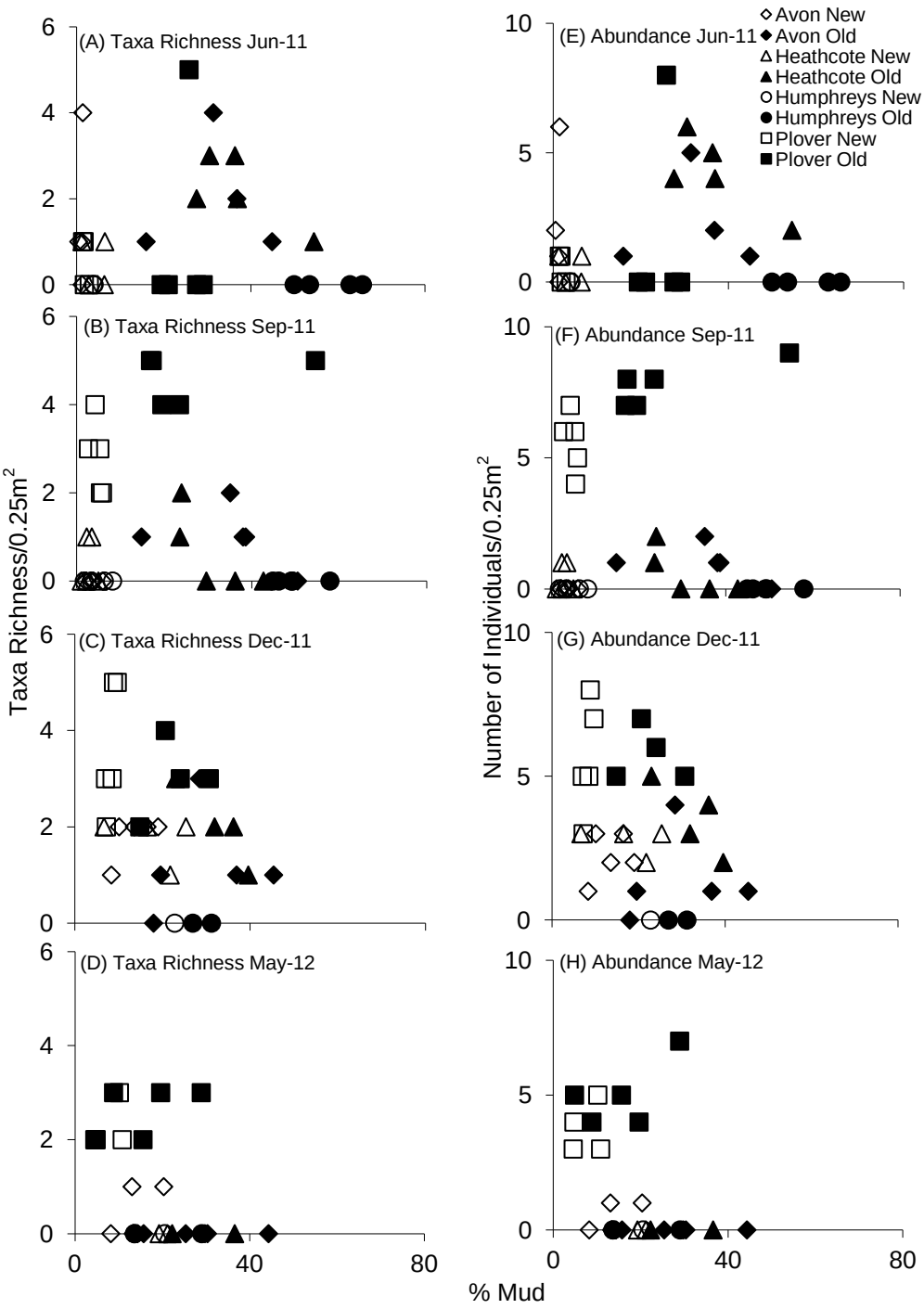

Figure 3.29. Scatterplots showing percentage mud (grain size <63µm) versus surface fauna taxa richness (A-D) and number of individuals (E-H) in old and new sediments across four sites and four sampling dates after the June 2011 earthquake.

3.3.5. Infauna

There were significant effects of site, sediment type, date and various interaction effects on infaunal community composition (Table 3.7). Infaunal taxa richness was,

Table 3.7. PERMANOVA analyses for infauna in old and new sediments sampled after the February 2011 (A) and June 2011 (B) earthquakes. For (A), site = fixed factor with six levels (Avon, Discharge, Heathcote, Heron, Humphreys, Plover); sediment type = fixed factor with two levels (old and new); sampling date = random factor with four levels (April/May 2011, September 2011, December 2011, May 2012). For (B), site = fixed factor with four levels (Avon, Heathcote, Humphreys and Plover), sediment type =fixed factor with two levels (old and new); sampling date = random factor with four levels (June 2011, September 2011, December 2011, May 2012). N=5 replicates per sediment type per sampling date per site.

(A) Feb-11 EQ

	DF	Pseudo-F	p
Site (Si)	5	8.39	**<0.001**
Sediment Type (ST)	1	8.72	**0.032**
Sampling Date (SD)	3	5.28	**<0.001**
Si*ST	5	3.26	**<0.001**
Si*SD	15	3.52	**<0.001**
ST*SD	3	1.97	**0.0056**
Si*SD*ST	15	1.22	0.081

(B) Jun-11 EQ

	DF	Pseudo-F	p
Site (Si)	3	13.28	**<0.001**
Sampling Date (SD)	3	4.82	**<0.001**
Sediment Type (ST)	1	11.21	**0.030**
Si*SD	9	2.20	**<0.001**
Si*ST	3	3.52	**0.0011**
SD*ST	3	1.34	0.15
Si*SD*ST	9	1.09	0.31

in general, similar between old and new sediments over time for sediments sampled after both the February 2011 and June 2011 earthquakes (Figs. 3.30 and 3.31). In the first sampling date after each earthquake, there were no instances where taxa richness was higher in new sediments than in old sediments. At Discharge, Heron and Plover, taxa richness was notably lower in new sediments than old sediments during this first sampling date. By May 2012, the taxa richness of new sediments at Avon and Plover was higher than the taxa richness in old sediments. Similar patterns were seen for the number of individuals between old and new sediments across sites. Despite the similarities of these variables between old and new sediments within sites, however, the taxa contributing to the richness and abundance were often different, particularly during the initial sampling date. Differences in infauna community composition among sites were also considerable (Table 3.8 and 3.9).

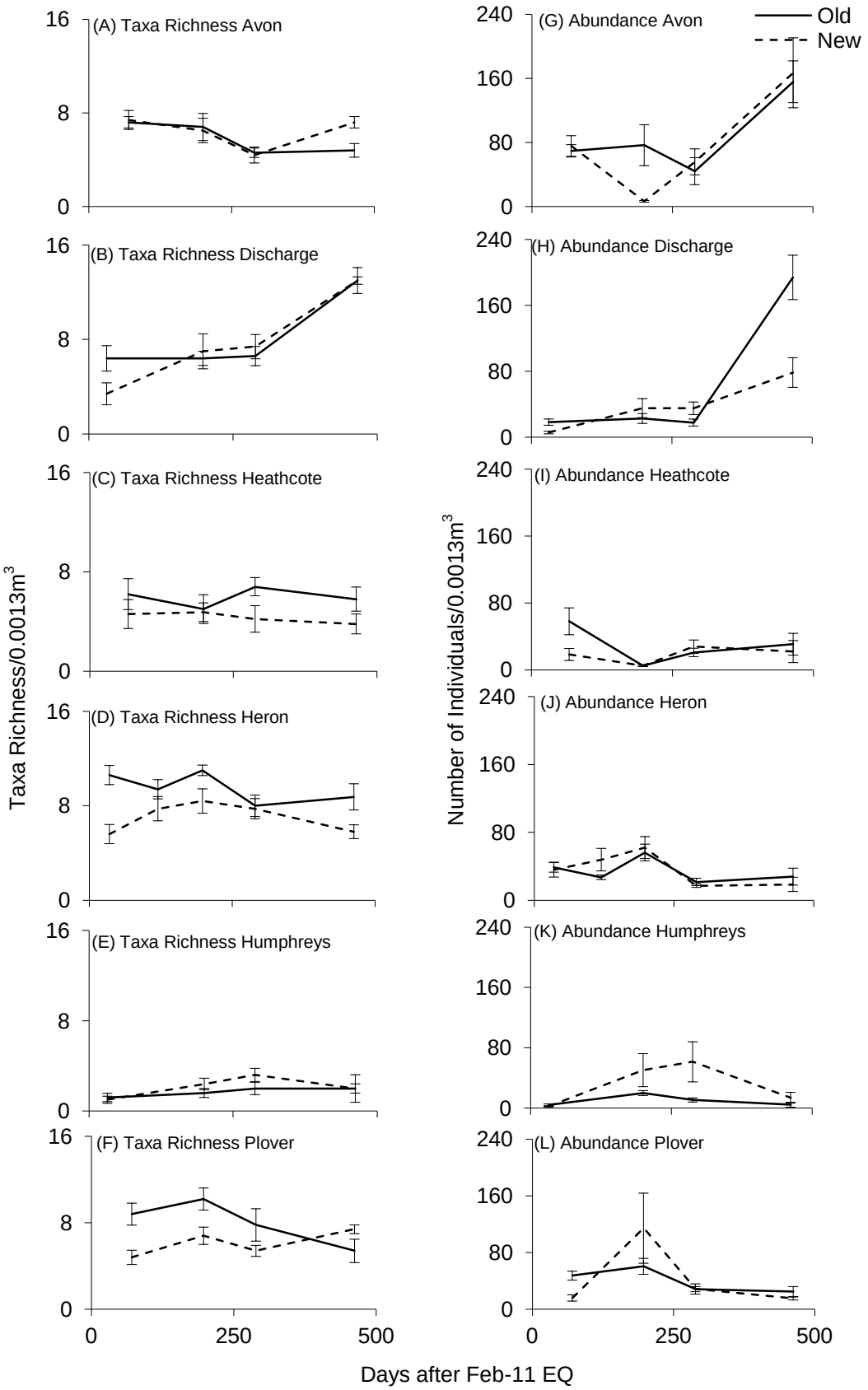

Figure 3.30. Average (±SE) taxa richness (A-F) and number of individuals (G-L) of infauna at six sites (Avon (A,G), Discharge (B,H), Heathcote (C,I), Heron (D,J), Humphreys (E,K) and Plover (F,L)) in areas of old and new sediment on sampling dates after the February 2011 earthquake. N=5 replicates per sediment type per sampling date per site.

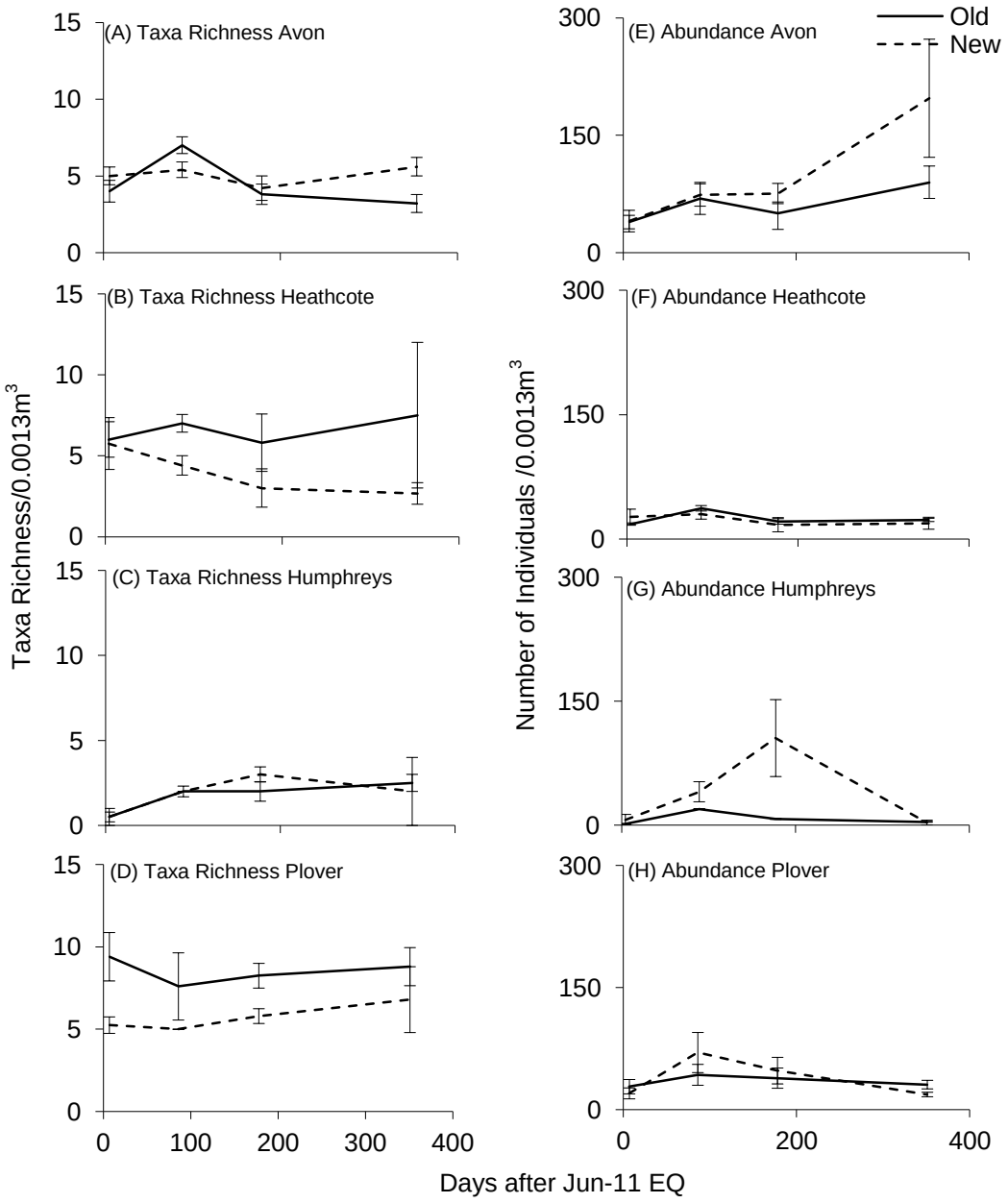

Figure 3.31. Average (±SE) taxa richness (A-D) and number of individuals (E-H) of infauna at four sites (Avon (A,E), Heathcote (B,F), Humphreys (C,G) and Plover (D,H)) in areas of old and new sediment on sampling dates after the June 2011 earthquake. N=5 replicates per sediment type per sampling date per site.

SIMPER analyses showed that, in general, there were similar species driving the community composition in old and new sediments but the number of species contributing to 90% of the community was less for new sediments than old sediments within a site during the initial sampling date after the earthquake (Table 3.7). The species composition of old and new sediments during the initial sampling date after the February 2011 earthquake was most similar at Avon, where *Arthritica* sp., *Potomopyrgus estuarinus* and *Nicon aestuariensis* dominated the community in both sediment types. This was also the case 15 months later. At Discharge,

Capitellidae were abundant in both old and new sediments during the initial and final sampling dates, and amphipods (*Paracalliope* sp., *Paracorophium* sp., *Phretogommarus* sp. and *Monocorophium* sp.) had become an abundant component of the community by the final sampling date. Capitellidae was the most abundant taxa in both old and new sediments at Heathcote and Humphreys. *Macropthalmus hirtipes* was abundant in old sediments at Heathcote but did not colonise new sediments until the final sampling date. *Aonoides* sp. was common in old and new sediments at Plover during the initial sampling date however not during the final sampling date when Capitellidae had become dominant. Across both sediment types and sampling dates, the "community" at Humphreys was comprised (>90%) of only one or two species (Table 3.8).

After the June 2011 earthquake, infaunal community composition differed significantly among sites, sampling dates and sediment types and two of the four interaction terms were significant (Table 3.9). Immediately after this earthquake, community composition in new sediments was not significantly different at four out of the six possible site combinations (Avon was significantly different to Heathcote and Plover). For old sediments however, community composition was significantly different across all sites. By September 2011, community composition in new sediments was significantly different between all sites, matching the patterns for old sediments at this same sampling date. By the final sampling date in May 2012, community composition was significantly different at four out of the six site combinations (not significant at Heathcote/Humphreys and Heathcote/Plover) for both new and old sediments.

Table 3.8. SIMPER analysis showing infauna contributing to 90% of the community at six sites (Avon, Discharge, Heathcote, Heron, Humphreys, Plover) 6-8 weeks and 15 months after the February 2011 earthquake in old and new sediments. N=5 replicates per sampling date per sediment type per site.

		Old Sediment			New Sediment		
		Species	Av.Abund	Contrib%	Species	Av.Abund	Contrib%
6-8 Weeks Post-EQ	**Avon**	*Arthritica* sp.	2.47	30.65	*Arthritica* sp.	2.04	24.98
		P. estuarinus	1.84	23.24	*P. estuarinus*	2.16	24.12
		N. aestuariensis	1.47	17.99	*N. aestuariensis*	1.31	16.29
		S. benhami	0.95	8.65	Capitellidae	1.47	11.43
		Capitellidae	0.84	8.32	*Paracorophium*	1.2	11.08
		Paracorophium	0.98	4.81	*A. crenata*	0.84	7.31
	Discharge	Capitellidae	1.55	37.87	Capitellidae	0.64	37.44
		M. hirtipes	1.25	31.97	*S. benhami*	0.68	29.05
		Arthritica sp.	0.82	7.99	*Scolepis*	0.76	20.68
		C. glandiformis	0.64	7.05	*Arthritica* sp.	0.44	7.2
		S. benhami	0.66	7.05			
	Heathcote	Capitellidae	2.09	44.09	Capitellidae	1.49	60.27
		M. hirtipes	1.05	15.34	*S. benhami*	0.77	14.24
		Arthritica sp.	1.23	15.2	*Paracorophium*	0.6	12.47
		A. stutchburyi	0.74	10.62	*Scolepis*	0.4	4.44
		Paracorophium	0.96	7.32			
	Heron	Capitellidae	1.71	18.1	*S. benhami*	1.47	26.53
		S. benhami	1.63	14.67	Capitellidae	1.44	26.43
		Sabelidae	1.48	14.59	*Scolepis*	1.64	24.69
		H. cylindrifer	1.36	13.72	*N. aestuariensis*	1.06	13.98
		N. aestuariensis	1.31	12.83			
		M. hirtipes	0.96	6.7			
		Scolepis	0.8	6.4			
		Nemertea Sp 1	0.7	3.48			
	Humphreys	Capitellidae	0.97	86.37	Capitellidae	0.52	100
		Anthropleura	0.56	13.63			
	Plover	*M. tenebrosus*	2.04	33.13	*M. hirtipes*	0.8	27.8
		Aonides sp.	1.8	26.82	*Aonides* sp.	0.85	19.51
		H. cylindrifer	1.12	12.73	*M. tenebrosus*	0.83	18.82
		A. stutchburyi	0.71	6.17	Capitellidae	0.66	13.44
		N. helmsi	0.75	5.67	*S. benhami*	0.64	13.4
		M. liliana	0.64	5.02			
		Paracorophium	0.7	5.01			
15 months Post-EQ	**Avon**	*Arthritica* sp.	3.39	53.44	*Arthritica* sp.	2.6	31.5
		N. aestuariensis	1.43	22.52	*P. estuarinus*	2.44	20.42
		P. estuarinus	1.44	20.35	*N. aestuariensis*	1.42	18.9
					S. benhami	1.1	14.06
					A. crenata	0.78	4.97
					Capitellidae	0.83	4.7
	Discharge	*Paracalliope*	2.29	15.91	Capitellidae	1.98	17.43
		Capitellidae	2.3	15.73	Paracalliope	1.78	14.09
		M. neozelanica	1.82	11.46	*Arthritica* sp.	1.16	10.57
		Arthritica sp.	1.89	10.72	*B. polybranchia*	1.27	10.52
		M. hirtipes	1.36	9.8	*H. cylindrifer*	1.14	10.45
		Paracorophium	1.65	8.44	*Paracorophium*	1.27	7.83
		Phretogammarus	1.51	5.69	*M. neozelanica*	1.23	6.58
		H. cylindrifer	0.9	4.99	*N. helmsi*	1	6.11
		N. helmsi	0.99	3.54	*M. hirtipes*	0.94	5.71
		Monocorophium	1.01	3.04	*Monocorophium*	1.01	3.81
		H. crenulatus	0.8	2.82			
	Heathcote	*Arthritica* sp.	1.14	27.84	*N. aestuariensis*	0.78	31.81
		S. benhami	0.68	14.1	*A. crenata*	0.6	21.5
		A. stutchburyi	0.64	13.52	*H. crassa*	0.48	15.97
		Halicarnus spp.	0.64	11.39	*Arthritica* sp.	0.46	10.39
		H. crenulatus	0.6	11.39	*M. hirtipes*	0.4	10.39
		N. aestuariensis	0.52	4.59			
		M. hirtipes	0.61	4.47			
		Megalope	0.44	4.31			
	Heron	*S. benhami*	1.13	21.72	Capitellidea	1.03	36.84
		A. stutchburyi	1.08	21.03	Scolepis	0.99	17.26
		H. cylindrifer	0.97	11.67	B. polybranchia	0.6	14.22
		Scolepis	1.12	10.53	H. cylindrifer	0.66	14.22
		Sabelidae	0.88	10.32	Arthritica sp.	0.57	7.89
		Hemipodus	0.75	9.81			
		Capitellidae	1.04	5.26			
	Humphreys	Capitellidae	0.59	100	Capitellidae	1.09	62.86
					Arthritica sp.	0.5	37.14
	Plover	*M. tenebrosus*	1.52	41.21	*S. benhami*	1.33	31.19
		Capitellidae	1.13	23.78	Capitellidae	1.11	26.07
		H. cylindrifer	0.86	19.7	*Scolepis*	0.8	7.8
		M. hirtipes	0.7	9.11	*N. aestuariensis*	0.64	7.7
					Arthritica sp.	0.66	7.61
					A. stutchburyi	0.64	7.61
					Sabelidae	0.44	2.69

Table 3.9. SIMPER analysis showing infauna contributing to 90% of community at four sites (Avon, Heathcote, Humphreys, Plover) 1 week and 11 months after the June 2011 earthquake in old and new sediments. N=5 replicates per sampling date per sediment type per site.

		Old Sediment			New Sediment		
		Species	**Av.Abund**	**Contrib%**	**Species**	**Av.Abund**	**Contrib%**
1 Week Post-EQ	**Avon**	*Arthritica* sp.	2.07	51.26	Capitellidae	1.45	26.83
		N. aestuariensis	1.55	37.58	*Paracorophium*	1.81	25.72
		P. estuarinus	1.04	6.39	*P. estuarinus*	1.55	24.03
					Arthritica sp.	1.05	10.42
					Scolepis	0.75	9.48
	Heathcote	*M. hirtipes*	1.43	38.21	*Scolepis*	1.14	34.59
		Capitellidae	0.96	19.88	Capitellidae	1.15	27.48
		A. stutchburyi	0.96	18.56	*Arthritica* sp.	0.87	23.48
		S. benhami	0.74	8.71	*H. cylindrifer*	0.75	8.21
		N. aestuariensis	0.7	7.96			
	Humphreys	All similarities are			All similarities are zero		
	Plover	*M. tenebrosus*	1.58	25.02	*Scolepis*	1.61	43.06
		Capitellidae	1.1	14.18	*Aonides* sp.	1.34	31.2
		Aonides sp.	1	13.54	Capitellidae	1.06	15.55
		M. hirtipes	0.9	10.29	*A. crenata*	0.55	3.4
		N. helmsi	0.92	10.27			
		M. liliana	0.6	6.58			
		H. cylindrifer	0.68	5.69			
		D. subrostrata	0.68	4.91			
11 Months Post-EQ	**Avon**	*Arthritica* sp.	2.7	64.91	*P. estuarinus*	2.93	35.77
		N. aestuariensis	1.17	22.8	*Arthritica* sp.	2.45	32.54
		P. estuarinus	1.49	12.29	*N. aestuariensis*	1.51	21.64
					A. crenata	0.83	4.83
	Heathcote	*Arthritica* sp.	1.59	56.82	All similarities are zero		
		M. hirtipes	1.16	43.18			
	Humphreys	All similarities are			All similarities are zero		
	Plover	Capitellidae	1.34	34.25	Capitellidae	1.15	26.08
		M. hirtipes	0.9	18.64	*S. benhami*	1.05	24.17
		M. tenebrosus	1.04	10.19	*A. stutchburyi*	0.75	12.9
		N. helmsi	0.68	9.87	*Aonides* sp.	0.7	11.84
		S. benhami	0.7	8.36	*Nemertea*	0.64	10.27
		M. liliana	0.55	4.32	*M. tenebrosus*	0.54	4.44
		Halicarnus sp.	0.55	4.03	*N. aestuariensis*	0.46	3.69
		Arthritica sp.	0.44	2.74			

SIMPER analyses showed that, in general, there were different species underpinning the community composition in old and new sediments, particularly during the initial sampling date after the June 2011 earthquake (Table 3.9). There were also clear site differences in species composition. Greater changes occurred in species composition between the initial and final sampling dates in new sediments than in old sediments. At Avon, there was a high abundance of Capitellidae in new sediments, but not old sediments, during the initial sampling date. However, by the final sampling date, Capitellidae had largely disappeared from the new sediments and the species composition of new and old sediments at this site had become very similar, dominated by *Arthritica sp.*, *Nicon* and *Potomopyrgus*. At Heathcote, *Macrophthalmus* were common in old sediments but not new sediments at both sampling dates. At Plover, the number of species contributing to 90% of the community in new sediments increased over time, from four species in the initial sampling date to seven species after 11 months. The number of species contributing to 90% of the community in old sediments at this site remained at eight over both

sampling dates and was largely composed of *Capitellidae*, *Microlenchus*, *Macrophthalmus*, *Aonoides* and *Scolecolepides benhami*.

PCO plots, based on distance from centroid data, showed that communities in old and new sediments become more similar to each other over time at some sites, most likely due to mixing of sediment types and convergence of organic content (Figs. 3.32 and 3.33).

Scatterplots of percentage mud versus taxa richness and number of individuals showed high variability but at the highest mud content of c. 60%, very few animals occurred (Figs. 3.34 and 3.35). Old and new sediments formed distinct clusters immediately after the earthquake event, with new sediments showing low amounts of percentage mud and old sediments showing more variable, but overall higher, amounts of percentage mud. Over time, mixing occurs as new sediments become muddier and show greater variability. There appears to be a ceiling factor with lots of variability at lower levels of mud content which begins to drop as mud content increases, i.e., mud content sets an upper limit to taxa richness/abundance and other processes (e.g., competition, predation) generate the variability below this ceiling.

MDS plots showed that all heavy metals and percentage algal cover were correlated with differences in surface faunal community composition among sites for Spearman's correlations >0.6 (Fig. 3.36A). For infauna, lead, zinc, arsenic and organic content were correlated with differences in community composition for Spearman's correlations >0.3 (Fig. 3.36B). In particular, these variables drove the separation of old and new sediments at Plover from sediments at the other sites.

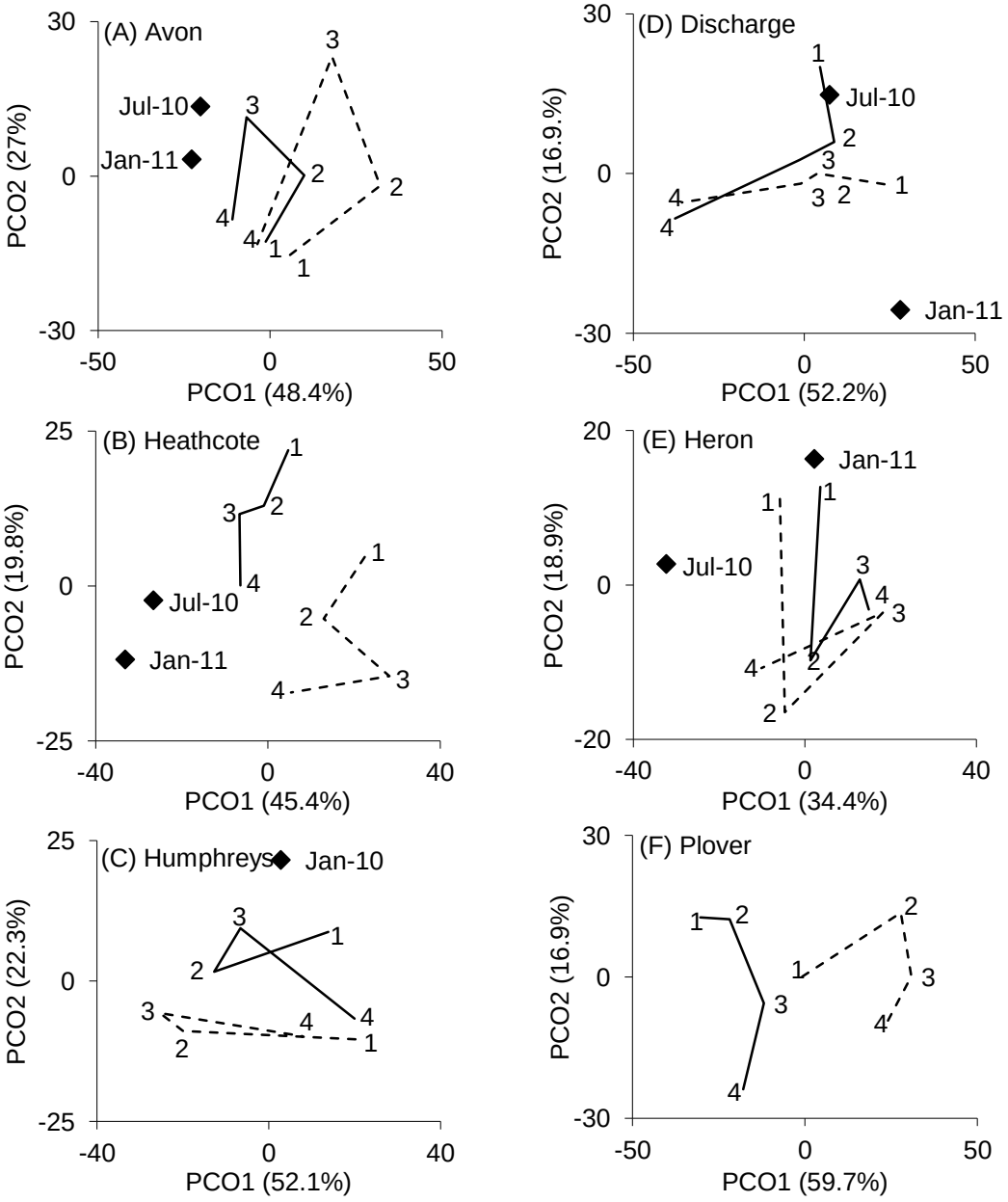

Figure 3.32. PCO plot based on distance from centroid data showing the trajectory of change of infaunal communities over four sampling dates (1=April/May 2011, 2=September 2011, 3=December 2011, 4=May 2012) at six sites (A-F) after the February 2011 earthquake. At sites where pre-earthquake data was available (taken from *Chapter 2*), the position of the community, in space, at July 2010 and January 2011 is shown. N=5. PCO1 and PCO2 values are percentage of total variation.

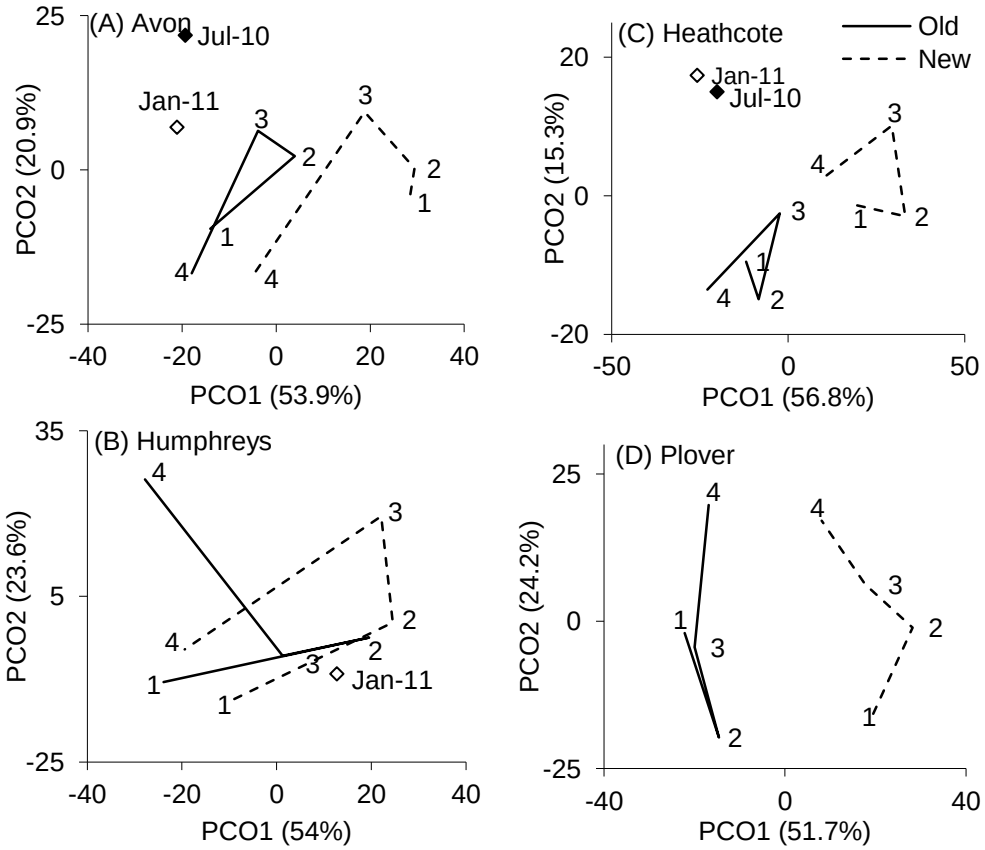

Figure 3.33. PCO plot based on distance from centroid data showing the trajectory of change of infaunal communities over four sampling dates (1=June 2011, 2=September 2011, 3=December 2011, 4=May 2012) at four sites (A-D) after the June 2011 earthquake. At sites where pre-earthquake data was available (taken from *Chapter 2*), the position of the community, in space, at July 2010 and January 2011 is shown. N=5. PCO1 and PCO2 values are percentage of total variation.

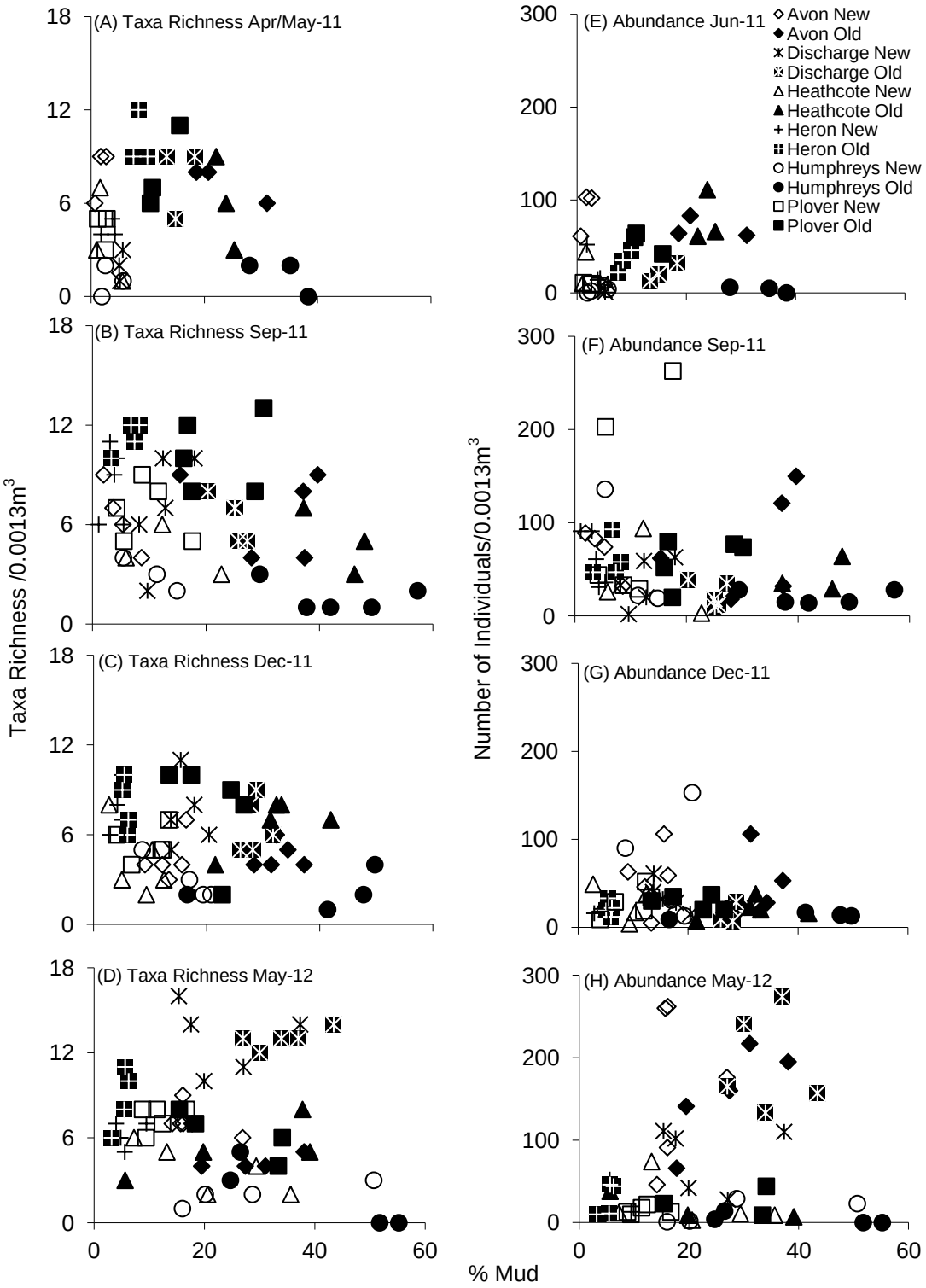

Figure 3.34. Scatterplots showing percentage mud (grain size <63µm) versus infaunal taxa richness (A-D) and number of individuals (E-H) in old and new sediments across six sites and four sampling dates after the February 2011 earthquake.

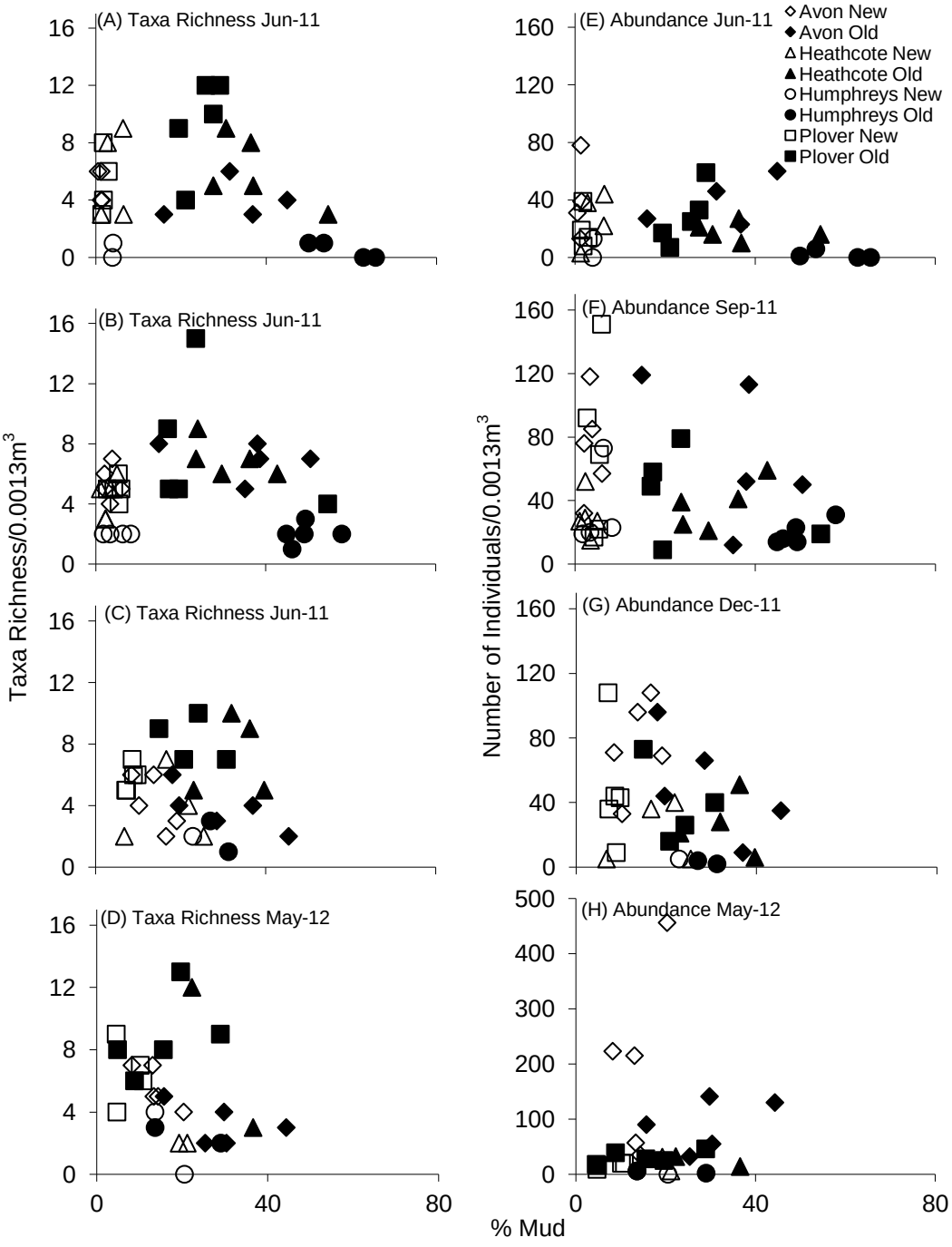

Figure 3.35. Scatterplots showing percentage mud (grain size <63µm) versus infaunal taxa richness (A-D) and number of individuals (E-H) in old and new sediments across four sites and four sampling dates after the June 2011 earthquake.

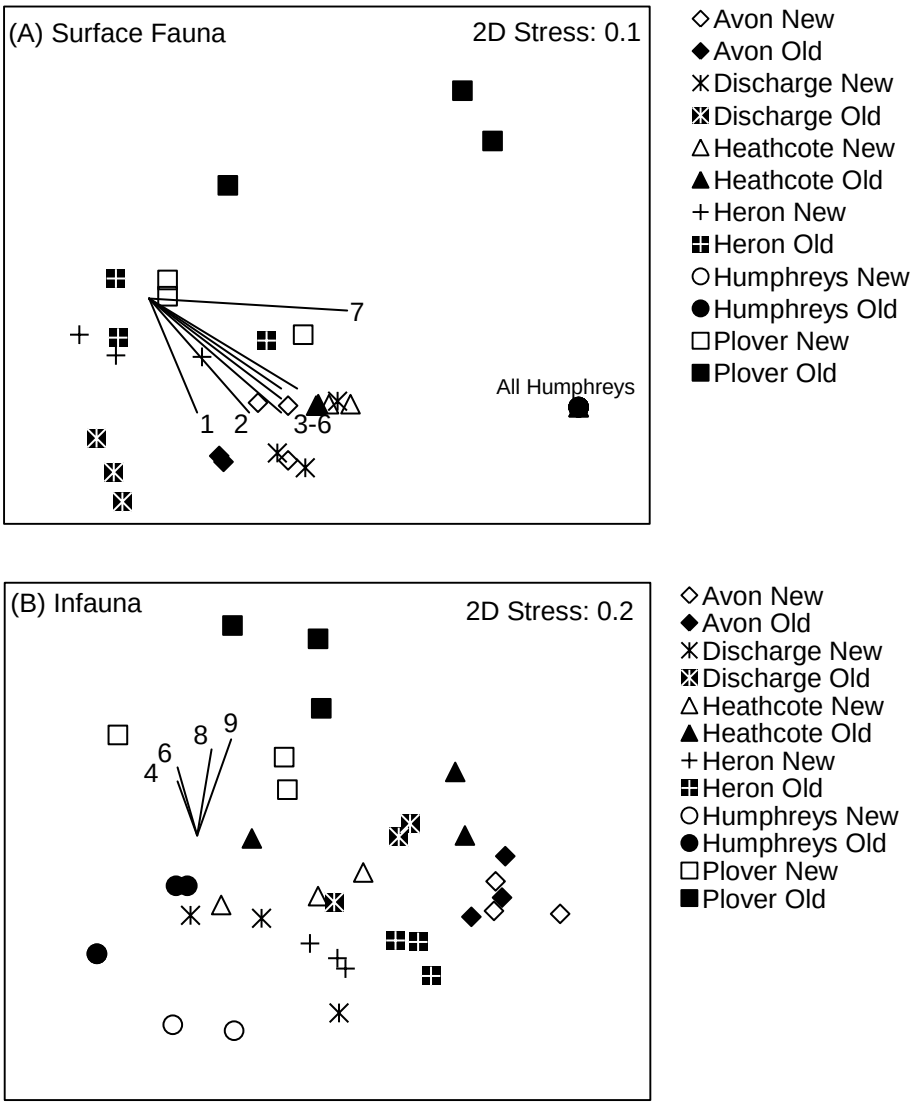

Figure 3.36. MDS plots showing surface faunal (A) and infaunal (B) community composition during the first sampling date (April/May 2012) after the February 2011 earthquake in old and new sediments at six sites. Vectors are overlaid to show the predictor variables driving composition for Spearman's correlations >0.6 (A) and >0.3 (B). 1=Chromium, 2=Nickel, 3=Copper, 4=Lead, 5=Cadmium, 6=Zinc, 7=Percentage algal cover, 8=Organic content, 9=Arsenic.

3.4. Discussion

The tilting and uplifting of the estuary floor, combined with the large amounts of liquefaction mounds, resulted in altered tidal flows and changes in the elevation and exposed areas of the Avon-Heathcote Estuary. New Zealand estuaries are generally shallow and intertidal and because of this, sediments are strongly influenced by processes occurring in the water column. This was the case here, where the old sediments reflected decades of nutrient and pollutant input particularly at sites on the

eastern side of the estuary (Humphreys and Discharge – see *Chapter 2*). Due to their cohesiveness, it is unlikely that these old organic-rich sediments dispersed much with tidal flows. Instead, it appears that the coarser sediments of the mounds dissipated over the old flats and mixed with surface sediments, becoming more contaminated and mixing their associated faunal and marine plant communities. This is supported by mound heights sequentially decreasing and communities in old and new sediments becoming more similar over time. In many places, this was seen by a thin film of new sediments covering old sediments as mounds flattened into each other. Mixing of sediments was likely driven not only by a complex combination of hydrodynamic features (e.g., tidal flows flattening and dispersing sediments), but also biological (e.g., bioturbation, burrowing) processes (Larsen and Macdonald 1993, Rainey et al. 2003).

Not all sites behaved the same and this was presumably related to tidal flows, currents, the coverage of mounds and their height. These site differences were expected as the sites were selected to represent a range of conditions within the estuary and were not chosen to be replicates of each other. For example, sites on the western side of the estuary, Heathcote and especially Humphreys, experience low tidal flows and reduced flushing. This has meant that organic matter and nitrogen have accumulated in these old sediments and, due to their cohesiveness, legacy effects will remain long after the cessation of inputs. In contrast, sites on the eastern side of the estuary, particularly Heron, and Plover, are exposed to more dynamic processes such as increased tidal flows and flushing. Here, old sediments are sandier and contain less organic matter. At these “cleaner” sites, the composition of old and new sediments was much more similar than at the eutrophic sites (Humphreys and Discharge).

Clearly, the earthquakes altered the natural trajectory of community and sediment recovery after the diversion. In particular, at the eutrophic sites, the recovery of the estuary may be accelerated due to the burial of a large portion of the polluted sediment that was previously exposed to the surface. For example, sediments at Humphreys were expected to take a long time to recover after the diversion due to high amounts of legacy nutrients and pollutants and low amounts of flushing and tidal flow at this site. But, the earthquakes did years of remediation of these sites in seconds by introducing large quantities of new sediments that capped the surface and buried the old sediments. This process of the capping is usually

implemented through human intervention to reduce legacy effects. It involves sealing eutrophic sediment off from the water column by placing a cover over the sediment to minimize the release of nutrients (or other pollutants). Experiments have been done using sand, gravel, or non-natural materials (e.g., zeolite, ceramicite, light porous media which react with and remove ammonium), to cap sediments (Wang et al. 1991, Zeman 1994, Huang et al. 2011). In some cases, 90-100% of total nitrogen in the overlying water has been removed by capping (Huang et al. 2011). The new sediments that covered 30-65% of the estuary floor after the earthquakes provided an example of capping, using natural materials (clean coarse sediments) and, unusually, occurring via natural processes. This example of capping is, however, different in that it was extremely patchy and occurred on a microscale resulting in significant within-site variation. As seen, there was considerable mixing and cross-contamination between old and new sediment patches over time.

3.4.1. Sediment properties

New sediments were found to cover 30-65% (site dependent) of the estuary surface during the first sampling period after the February 2011 earthquake. These estimates are higher than those presented by Measures (2011) who found 20-40% of the estuary bed to be covered in new sediments. These authors, however, used aerial survey (fixed wing) imagery of the estuary which, while obtained at high resolution (10cm), was probably less accurate than ground-based studies in resolving the edges of the new sediments. Inconsistencies may also be due to the fact that work by Measures (2011) occurred on 24 February 2011 whereas my first sampling period was 31-70 days (site dependent) after the February earthquake, providing time for the redistribution of old and new sediments. The height of new sediments during this first sampling period after the February earthquake were considerably lower than the initial heights of new sediments produced by the June earthquake. I was able to sample almost immediately after the June event, and so have very accurate ground-based measurements of new mounds. Mound heights sequentially decreased as tidal flows flattened and dispersed sediments between earthquakes. However, not all sites behaved the same, presumably related to tidal flows and currents.

Contamination by heavy metals can be a complex process involving site-specific characteristics, legacy effects, and recent inputs. In the case of the Avon-Heathcote Estuary, the greatest differences after the earthquake events were

aligned with old and new sediments. New sediments were relatively pristine, having come from probably ancient alluvial sediments sequestered below the estuary floor. Old sediments, however, clearly differed among sites in chemical contamination. This likely reflects the pollution gradient present in the estuary prior to the earthquake due to years of heavy metal accumulation in old sediments. The differences may also be driven by differences in grain size among sites, as finer grained sediments have been shown to have higher concentrations of heavy metals than sandier sediments (Tam and Wong 2000). This is due to the larger surface area of coarser sediments which binds metals less strongly (Bridges 2005). Differences in grain size may also account for the reduced heavy metal concentrations in new versus old sediments. However, it is also likely that the new sediments, which were exhumed from deep below the estuary surface, had consequently been relatively unexposed to metals pollution occurring in the estuary over the last century.

Based on the total organic carbon condition ratings developed for estuaries in Southland New Zealand (e.g., Robertson 2006) the organic content of new surface sediments immediately after the earthquakes fell within the good (<2% organic content) range. Old sediments were more variable, with values in the fair (2-5% organic content) and good ranges. Values of >5% seen at Humphreys are considered to be of poor condition. The levels of organic matter measured in old sediments after each of the earthquakes were similar to those measured in June and December 2010 during the sampling done in *Chapter 2*. This, combined with the reduction in the organic content of old sediments over time, indicates that the influx of new organic matter after the February earthquake, resulting from the breakdown of the city's wastewater and sewage system, was not incorporated into the surface sediments in any significant quantity (i.e., not significant relative to pre-existing content indicating that the legacy effects of sediment organic matter seem to be over-riding any immediate earthquake effects). Over time, the organic content of old and new sediments became more similar (new sediments increasing and old sediments decreasing in organic content) and at some sites converged, indicating mixing of surface sediments. It was not surprising to find no difference between the organic content of surface old sediments and that of the old (buried) surface of the new sediments, as well as no differences between old and new sediments at 30 and 60cm below the surface within sites. This indicates that few, if any, new sediments

became incorporated into the existing old sediments at various depths below the surface when they erupted up to the surface during the earthquakes.

3.4.2. Biological properties

There are a range of physical, chemical and biological factors, such as grazing, nutrient availability, physical disturbance depth, light flux and sediment characteristics that can regulate BMA biomass in shallow aquatic ecosystems (MacIntyre et al. 1996, Cahoon et al. 1999). Sediment grain size has been reported to be an important factor controlling the distribution and abundance of BMA (Pomeroy 1959, Brotas 1995, Jesus 2009) although there are conflicting reports as to the nature of this relationship. Some studies report negative relationships between grain size and BMA biomass, i.e., a reduction in biomass occurring in finer sediments (Riznyk and Phinney 1972, Colijn and Dijkema 1981, Davis and McIntire 1983, Shaffer and Onuf 1983, Fielding et al. 1988, Cahoon et al. 1999) whereas others report positive relationships, concluding that BMA assist in the stabilisation of fine sediments (McIntire and Amspoker 1986, Cahoon et al. 1999). In the current study, the percentage cover of benthic microalgae (BMA) was generally higher on new sediments than old sediments supporting a positive relationship between grain size and biomass (or, in this case, percentage cover). This may be due to new sediments having fewer grazers, lower concentrations of heavy metals, enhanced light penetration (allowing light to reach BMA deeper in the sediment) and lower levels of organic matter (high levels of organic matter have been shown to provide a less favourable and more anoxic habitat for BMA due to increases in oxygen demand and heterotrophic bacteria from the decomposition of organic matter (Barnes 1984, Bolam 2000)).

The higher percentage cover of *Gracilaria* and *Ulva* at some sites, during the summer of December 2011, was not unexpected due to the algal blooms that have historically occurred in the estuary during the summer months (Barr 2012). These are likely fuelled by the increased irradiance and warmer seawater temperatures in spring which facilitates the germination and growth of propagules, resulting in a higher biomass during summer months (Dan et al. 2002). The absence of *Zostera* at the more eutrophic sites was not surprising as it is well-known that high levels of nutrient loading reduce the growth rates and survival of seagrass species (Short et al. 1995, Bostrom et al. 2002, Hauxwell et al. 2006, Baeta et al. 2009b, van Katwijk

et al. 2010). Despite areas of relatively low nutrient new sediments occurring, these were situated within eutrophic old sediments and the mixing of new and old sediments, as well as the lack of close-by propagules, likely prevented the colonisation of *Zostera* in new sediments at the more eutrophic sites.

The extent to which faunal communities are impacted by disturbance depends on the effects that the disturbance has on the key environmental gradients, such as salinity, dissolved oxygen, sediment grain size, exposure, shore level and sediment chemistry, that structure communities in a particular area (Whitlatch 1977, Raffaelli 1996, Dittmann 2000, Little 2000). Interestingly, in this study, taxa richness and the number of individuals of surface fauna were similar between new and old sediments after the earthquakes and, in general, remained similar to each other as they changed through time. Compared to pre-earthquake levels, however, the taxa richness and particularly number of individuals were generally lower after the earthquakes than they were compared to surveys done in July 2010 and January 2011 (see *Chapter 2* for pre-earthquake data). Pollution can adversely affect marine fauna by altering assemblages and reducing diversity (Agard et al. 1993, Warwick and Clarke 1995) and thus it is possible that the large discharges of raw effluent into the estuary after the earthquakes may have killed some taxa, reducing overall richness and abundance regardless of sediment type. Long sediment cores also showed that many surface fauna were buried under the new sediments. Consequently, it is possible that re-colonisation of the new sediments between the February earthquake and the first sampling date effectively diluted the numbers of individuals remaining on the old sediments, as they equilibrated their densities between old and new sediments through migration onto the new sediments. This could account for the approximately equal densities of surface fauna between the two sediment types and the reduced abundance on old sediments relative to pre-earthquake surveys. Furthermore, the large area of the estuary covered in new sediments would have provided large amounts of new areas to colonise. Despite similar levels of taxa richness and number of individuals between old and new sediments, the species composition was not always the same between sediment types within a site. This suggests that some taxa may have exhibited a preference for their old “usual” (pre-earthquake) habitat rather than a new habitat that had a different composition and chemistry.

Taxa richness and number of individuals of infauna were also similar between new and old sediments after the earthquakes and, in general, covaried together through time. The species composition of old and new sediments was, however, generally very different within sites. Immediately after the earthquakes, infaunal taxa richness in old sediments was higher at Plover and Heron, likely reflecting their increased distance from the historically most polluted areas. Humphreys, the most eutrophic site, had very few infaunal species, reflecting the severe degradation of this area and also likely the dense algae mats that were present at this site for much of the study period. Dense algae cover can lower sediment oxygen levels and increase the amount of sulphur, ammonium and organic matter in the sediment, which can be toxic to benthic communities at specific thresholds (Hull 1987). In contrast, in areas where algae is present but in a lower abundance, infaunal densities may increase due to an increase in food supply. High numbers of polychaetes from the opportunistic Capitellidae family were found at Humphreys and Discharge. This is to be expected as these individuals are pioneering colonists that flourish and dominate assemblages in highly polluted and disturbed areas (Kitamori 1975, Pearson and Rosenberg 1978, Kikuchi 1979). It was interesting that Capitellidae were present in new sediments at these eutrophic sites despite their relative “pristine” state. This finding, as well as similarities seen between the species composition of old and new sediments at other sites, supports the hypothesis that the new sediments are being colonised by species present in the surrounding old sediments.

Patterns of succession are complex and can be driven by a large number of factors including the development of larvae, supply/pool of potential colonists and the dispersal potential and settlement of larvae and post-larvae forms (lateral advection), biotic interactions such as competition, facilitation, tolerance, food resources, predation and parasitism, mortality cycles, the availability of food, physiochemical factors such as oxygen levels, temperature and salinity and flow rates, wind/wave action, hydrodynamics and sediment composition. The appropriate habitat and the scale, duration and timing of the disturbance and season, resident fauna and their density and behaviour are also important (Connell and Slatyer 1977, Pearson and Rosenberg 1978, Zajac and Whitlatch 1982a, b, Zajac et al. 1998). The results from this chapter have shown sediment type (which encompasses sediment composition/chemistry, nutrient concentration) to have a significant impact on both

infauna and surface fauna community composition. The study shows that the colonisation of new sediment areas is closely related to the species composition of nearby ("pool") habitats, at least initially. However, the relatively quick (~2 years) recovery of fauna communities in old and new sediments to pre-earthquake status, supports literature which states that populations may persist or recover from disturbances at a rate which is fast enough to prevent long-term persistent impacts (Holling 1973, Underwood 1989). The effects of the earthquake were also highly site dependent, supporting Jones (1992) and Luoma (1989) who propose that environmental impacts vary among habitats. This may be due to distance from the impact/differences in intensity between habitats and/or spatial differences in the resistance of populations and assemblages (Holling 1973, Underwood 1989).

3.4.3. Summary

Soft-sediment habitats and their assemblages are heterogeneous due to strong structuring forces of stress and disturbance. Understanding the spatial and temporal extent, intensity and duration of disturbance on habitats and whole ecosystems is important in determining the effects on local environments and communities. The results of this chapter highlight the significant physical, chemical, biological and ecological impacts that the earthquakes had on the Avon-Heathcote Estuary. Consistent with my hypotheses, new sediments were coarser, had lower concentrations of heavy metals and less organic matter than new sediments. They also had fewer inhabitants initially but this increased over time. I did not, however, expect to find such low levels of faunal richness and abundance in old sediments after the earthquake events. The results supported my hypothesis that over time, new sediments would be colonised by fauna in neighbouring sediments and that there would be a strong site effect that was much more pronounced in old, relative to new, sediments.

Overall the results of this chapter are consistent with disturbance-colonisation models that predict a reduction in taxa richness in disturbed and/or polluted areas coupled with an increased abundance of opportunist species. I have demonstrated that habitat change, in this case resulting from a natural disturbance, can greatly affect the physical and biological structure of estuarine ecosystems. With aquatic habitats being continually altered by natural disturbances and increasingly subjected

to anthropogenic stresses, understanding the impacts of disturbance events on estuarine and coastal habitats and communities is of great ecological importance.

Chapter Four

Pathways of Carbon and Nitrogen Flow through an Estuarine Food Web in response to Eutrophication and Disturbance

4.1. Introduction

Eutrophication and disturbance events can severely impact the diversity and abundance of primary producers and consumers in estuarine systems and, in turn, alter trophic interactions and change the structure of entire food webs (Rau et al. 1981, Spies et al. 1989, Gearing et al. 1991, McClelland and Valiela 1998, Lotze and Milewski 2004, Armitage and Fourqurean 2009). Estuarine habitats are particularly susceptible to changes in trophic structure from eutrophication and/or disturbance due to close physical links to terrestrial habitats and the input of terrestrial organic matter into estuarine food webs (Martinetto et al. 2006, Shurin et al. 2006). Furthermore, estuaries are well-known nursery grounds that can sustain a high abundance and diversity of species, whose recruitment, growth and survival are closely linked to the quality and availability of food sources. This, in turn, depends on the quality of the habitat and its external inputs. Theoretical models have shown that food chains are shorter in disturbed environments as frequent or severe disturbance events such as eutrophication prevent longer chains from forming (Singer and Battin 2007, Tewfik et al. 2007). But, as each eutrophication/disturbance case is unique, understanding impacts requires an assessment of entire communities, producers and consumers, and the links within them (Armitage and Fourqurean 2009).

Increases in dissolved inorganic nitrogen (DIN), particularly ammonium, to aquatic environments can increase the biomass of primary producers (Kinney and Roman 1998) and therefore the overall food supply. Because fewer primary producers are able to withstand and survive eutrophic conditions, however, producer diversity is generally reduced, resulting in fewer food types available to consumers. For example, fast-growing ephemeral macroalgae such as *Ulva* spp. can flourish under high nutrient conditions, replacing slower growing perennial algae and seagrass (e.g., Howarth 1988, Short and Wyllie-Echeverria 1996). Exposure to a greater number of food sources does not necessarily result in more food sources being incorporated into consumer diets; palatability, digestibility, nutrient status, abundance, competition and consumer feeding guilds are important factors in determining the amount of assimilation of a particular food source. In general, phytoplankton, benthic microalgae (BMA) and many macroalgae (note that significant variations in palatability exist within macroalgae; Heckscher et al. (1996)) are considered to be more attractive food sources due to their high nutrient status and easy to digest tissues. In comparison, the lower nutrient tissues and structural

cellulose that exist in seagrasses render these plants a less attractive food source for consumers (McClelland and Valiela 1998).

Trophic interactions are complex and without quantitative analyses, it is difficult to predict how changes in primary producer assemblages will affect the structure of entire estuarine food webs. Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have been widely used to investigate food web structure and changes in trophic status resulting from eutrophication and disturbance events (McClelland and Valiela 1998, Voss et al. 2000, Martinetto et al. 2006, Pruell et al. 2006, Hadwen and Arthington 2007, Fox et al. 2009 amongst others). Features and applications of these two isotopes are discussed below.

Carbon ($\delta^{13}C$) Stable Isotopes

Carbon stable isotopes ($\delta^{13}C$) represent the ratio of ^{13}C:^{12}C. Of all the carbon atoms present on earth, ^{12}C accounts for 98.89% with ^{13}C accounting for only 1.11% (Killops 2005). These isotopes are used to determine consumer food sources due to primary producers often (but not always) having unique $\delta^{13}C$ values that are passed on to their consumer, generally to within 0.5-1‰ (parts per thousand) of their food source (DeNiro 1978, Wada et al. 1991). This range of values is due to taxonomic differences and impacts of the physical environment altering carbon fractionation (Wiencke and Fischer 1990, Raven et al. 2002). In estuarine systems, an average $\delta^{13}C$ enrichment of +0.5‰ with each increasing trophic level has been reported (Peterson and Fry 1987, France and Peters 1997). Consumers assimilating more than one carbon or food source will have a $\delta^{13}C$ value intermediate of those food sources, reflecting the relative proportions in which each carbon/food source was assimilated.

The $\delta^{13}C$ values of primary producers are influenced by the dissolved inorganic carbon (DIC) “end-member sources” that they are exposed to. In estuarine environments, possible DIC end-member sources include the ocean, rivers and other anthropogenic point source (e.g., sewage) or diffuse (e.g., fertiliser) inputs. The DIC “pool” characteristic of each of these end-members can be contributed to by several DIC sources, including CO_2, HCO_3^-, CO_3^{2-} and H_2CO_3. The amount of DIC contributed by each of these components depends on water characteristics such as pH, temperature, depth and salinity, as well as spatial and temporal influences (Mook 1991). The $\delta^{13}C$ values of primary producers are determined not only by their

location relative to end-member sources, but also by their affinity for carbon from each of the different sources they are exposed to, metabolic pathways, fractionation, temperature, growth rate, pH, salinity and species type (Sackett et al. 1965, Wada 1978, Wong and Sackett 1978, Takahashi et al. 1990, Hinga et al. 1994, Korb et al. 1996). In general, terrestrial plants have more depleted $\delta^{13}C$ values than marine plants and algae. For example, C_3 (fix CO_2 to form 3-phosphoglycerate) and C_4 (fix CO_2 to form oxaloacetate) terrestrial plants have $\delta^{13}C$ values around -26‰ (Park 1961) and -14‰ (O'Leary 1988) respectively. In comparison, seagrasses, C_3 plants in the marine environment, have $\delta^{13}C$ values spanning -15 to -3‰ (Zieman et al. 1984, Wada 1990, Yamamuro 1999) and phytoplankton (that, dependent on species, can use both C_3 and C_4 pathways), in natural seawater, range from -20 to -30‰. Overall, more enriched $\delta^{13}C$ values indicate there is more autochthonously (marine) produced carbon (i.e., in the ocean) and more depleted $\delta^{13}C$ values indicate more allochthonously (terrestrially) produced carbon (i.e., rivers, sewage).

The use of $\delta^{13}C$ in ecological studies is limited by trophic fractionation, variability in food source signatures and overlap in signatures of potential food sources, all of which can make data difficult to interpret (Gannes et al. 1997, Post 2002). Thus to gain a thorough understanding of entire food web structure, it is essential that $\delta^{13}C$ values of food sources and lower trophic levels are first accurately determined.

Nitrogen ($\delta^{15}N$) Stable Isotopes

Nitrogen stable isotopes ($\delta^{15}N$) represent the ratio of ^{15}N to ^{14}N, that account for 1% and 99% of all nitrogen atoms respectively (Killops 2005). Nitrogen in the marine environment is composed of nitrogen gas, dissolved inorganic nitrogen (DIN; ammonium, nitrate, nitrite) and organic nitrogen (Voss 2011). In ecological studies, nitrogen stable isotopes have two key applications. The first is to estimate the trophic position of organisms within a food web, as consumers are generally enriched by 3-4‰ relative to their food source/s. This fractionation occurs because of the preferential assimilation or transformation of ^{14}N due to it being lighter, easier to metabolise and of greater abundance relative to ^{15}N which is retained at a much higher rate (Wada et al. 1991, Post 2002). The second important application of $\delta^{15}N$ is that it can be used to distinguish between nitrogen sources, particularly the end-members contributing nitrogen to a system. End-members, such as the ocean,

rivers, fertilisers and sewage, generally have unique $\delta^{15}N$ values that make it possible to track the amount of incorporation of each source into the tissues of primary producers and consumer organisms. In general, nitrogen resulting from anthropogenic inputs (sewage) is enriched in $\delta^{15}N$ relative to natural nitrogen sources in the system. This is due to ammonium volatilisation and denitrification processes during sewage treatment that remove the lighter $\delta^{14}N$ faster than the heavier $\delta^{15}N$ (McClelland and Valiela 1998, Cole et al. 2004, Cole et al. 2006). Untreated sewage, or sewage that has been treated by methods that do not involve ammonium volatilisation or denitrification, has depleted $\delta^{15}N$ values, generally between 1.8 and 2.5‰ (Sweeney et al. 1980, Spies et al. 1989, Van Dover et al. 1992).

In general, the $\delta^{15}N$ values of primary producers and consumers can indicate the amount of eutrophication occurring in an area because they incorporate different nutrient sources into their tissues. For example, fast-growing *Ulva* spp. can reflect levels of nitrogen loading in particular areas (Barr et al. 2013). One limitation of using $\delta^{15}N$ values of primary producers and consumers to infer information about nitrogen sources is that some algae, especially microalgae, can fractionate widely against nitrogen isotopes because of the effects of light, temperature and nutrient availability/source (Wada 1978, Waser et al. 1998, Needoba et al. 2004). Thus, $\delta^{15}N$ values must always be interpreted with caution with this issue of fractionation in mind.

Benthic fauna from eutrophic areas have been shown to have isotopic values that are distinct from fauna at non-impacted sites, thereby showing that sewage-derived material can become incorporated into marine food webs (e.g., Rau et al. 1981, Spies et al. 1989, Gearing et al. 1991, Van Dover et al. 1992). Many studies using stable isotopes to examine the effects of eutrophication have focused exclusively on primary producers within a system (e.g., McClelland and Valiela 1998, Cole et al. 2004, Savage and Elmgren 2004, Lapointe et al. 2005, Thornber et al. 2008, Lapointe et al. 2011, Viana et al. 2011, Barr et al. 2013) and often on one isotope, usually $\delta^{15}N$ (e.g., Cole et al. 2004, Lapointe et al. 2005, Thornber et al. 2008, Lapointe et al. 2011, Viana et al. 2011, Barr et al. 2013). Studies on consumers often examine the isotopic signature/s of one or several consumers without considering their food sources (e.g., Pruell et al. 2006, Mallela and Harrod

2008, Oczkowski et al. 2008, Fertig et al. 2009), or focus on only one or two consumers and their potential food sources (e.g., Rogers 2003, Allan et al. 2010). Studies examining all major food sources and consumers in a system, particularly in response to eutrophication, are more rare (e.g., Keats et al. 2004, Martinetto et al. 2006, Baeta et al. 2009a, Olsen et al. 2011). Furthermore, there are very few studies that incorporate long-term temporal monitoring of systems as they become more or less eutrophic. Examples include Tucker et al. (1999), who tracked the incorporation of sewage-derived material into food webs in Boston Harbour and Massachusetts Bay following the abatement of inputs, and Rogers (2003), who monitored the trophic recovery of flora and fauna following the closure of an ocean outfall at Moa Point in Wellington, New Zealand, although the duration of this study was only nine months.

From 1973 to March 2010, Christchurch's sewage was tertiary-treated and this treated effluent discharged diurnally on the ebb tide into the Avon-Heathcote Estuary (up to 500,000m^3 of wastewater was discharged into the estuary each day) (URS 2004). The process of sewage treatment was, however, by biological oxidation (i.e., carbonaceous treatment) and did not nitrify ammonia and produce nitrates for denitrification (James Feary, Water and Wastewater Treatment Manager, pers. comm.). Consequently, the ammonium concentration of the wastewater essentially remained consistent throughout the treatment process. Based on this, the isotopic values of nitrogen should have been similar to that of raw sewage (i.e., low/depleted $\delta^{15}N$ values) rather than higher values that would be expected in tertiary treated sewage that is subjected to denitrification processes. After March 2010, the wastewater was still treated in this manner but discharged offshore. Examining the effect of the diversion on the isotopic chemistry of the estuary was one of the objectives of this chapter.

The Avon-Heathcote Estuary was also affected by the earthquakes in 2011 as outlined in the *General Introduction* and *Chapter 3*. After the February and June 2011 earthquakes there were large areas of liquefaction, "new sediment," and large quantities of raw sewage (expected to have low isotopic values) entered the estuary from multiple locations until 28 October 2011 (see *Chapter 3 Introduction* for details). The effects of the liquefaction and raw sewage on the isotopic chemistry of the estuary were also examined in this study.

In this chapter, I aimed to determine whether the $\delta^{13}C$ and $\delta^{15}N$ values of all major food sources and consumers vary spatially and temporally and reflect changes

in nitrogen input and sources to the Avon-Heathcote Estuary resulting from the offshore diversion of wastewater and earthquake events. In particular, I addressed three key questions: 1) Do $\delta^{13}C$ and $\delta^{15}N$ values of primary producers and consumer organisms vary spatially, temporally and in response to nitrogen/organic loading?, 2) Are primary producers at the same site receiving nitrogen from the same source?, and 3) What are the dominant food sources contributing to the diets of consumers and do these change spatially, temporally and in response to nitrogen/organic loading?

I hypothesised that:

- Food sources and consumers from the most eutrophic site ("Discharge") would have isotopic values that were more depleted (lower) than food sources and consumers at other sites situated near the rivers or the estuary mouth. Mechanistically, this would be driven by a higher uptake of depleted sewage-derived carbon and nitrogen by the primary producers at Discharge that was then passed on to consumer organisms.
- Spatial differences in the isotopic values of food sources and consumers would decrease after the diversion due to the cessation of sewage inputs to the estuary.
- Isotopic values of food sources and consumers would become more depleted after the earthquakes due to the uptake of raw sewage by primary producers, and in turn, consumers.
- Primary producers at the same site would be receiving nitrogen from the same source, likely a combination of pelagic and sediment DIN and DIC sources. I expected differences in the isotopic values of primary producers, particulate organic matter (POM) and consumers among the most eutrophic site (Discharge), the river sites, and the sites closest to the estuary mouth, due to isotopic variations in the different end-member DIC and DIN pools.
- Benthic microalgae (BMA) would contribute a large component of the diet of the mudsnail *Amphibola crenata*, POM would be the dominant food source of the cockle *Austrovenus stutchburyi* and the three crab species (*Austrohelice crassa*, *Hemigrapsus crenulatus* and *Macrophthalmus hirtipes*) would

consume a combination of macroalgae and benthic POM, across all sites and time periods.

4.2. Methods

4.2.1. Study sites

Samples for $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis were collected on various sampling occasions from December 2009 to August 2012 at a number of sites within and around the Avon-Heathcote Estuary. Table 4.1 summarises the food sources and consumer organisms that were sampled and the sites and dates they were collected. The location and characteristics of all sites are given in *Chapter 1: General Introduction.* Briefly, Discharge was situated below the former discharge pipe that, prior to March 2010, discharged high quantities of tertiary treated wastewater into the estuary. Discharge, alongside Humphreys, that was situated in a low-flow "back-water" area of the estuary close to Discharge, were the most eutrophic sites, historically receiving high amounts of sewage-derived DIC and DIN. Avon and Heathcote were situated within the estuary at their respective river mouths and consequently exposed to greater amounts of riverine and terrestrial inputs. Heron and Pukeko were nearest the estuary mouth and the channel and flow patterns within the estuary meant these sites were most greatly influenced by marine processes. Fish samples were collected from six different sites: Mt Pleasant (near Heathcote), Ponds (near Discharge), Pleasant Point (near Avon), Ebbtide St (near Heron), Tern St (near Pukeko) and Shag rock (at the estuary mouth). The locations of all sites are shown in *Chapter 1: General Introduction*.

Table 4.1. Collection dates and sites for the different food sources and consumers sampled for $\delta^{13}C$ and $\delta^{15}N$. Note that not all food sources/consumers could be found at all the sites and dates given.

Sample Type	Dates Collected	Sites Sampled
Cockles, Mudsnails, Crabs, Sediment: *Austrovenus stutchburyi, Amphibola crenata, Hemigrapsus crenulatus, Macrophthalmus hirtipes, Austrohelice crassa,* Sediment POM	Dec-09, Feb-10, Apr-10, Jul-10, Oct-10, Jan-11, Apr-11, Jul-11, Oct-11, Jan-12, Apr-12, Jul-12	Avon, Discharge, Heathcote, Heron, Pukeko
Fish: *Aldrichetta forsteri, Rhombosolea plebeian*, *Retropinna retropinna*	Dec-10, Dec-11	Ebbtide St, Mt Pleasant, Pleasant Pt, Ponds, Shag Rock, Tern St
Polychaetes	Jan-11, Jan-12	Avon, Discharge, Heathcote, Heron
Microlenchus tenebrosus, Diloma subrostrata	Jan-11, Jan-12	Heron
Cominella glandiformis	Jan-11, Jan-12	Pukeko
Pelagic POM	Dec-09, Apr-10, Jul-10, Apr-11, Jun-11, Aug-11, Dec-11, Apr-12, Aug-12	Treatment ponds, Avon River, Heathcote River, Estuary Mouth
Benthic microalgae (BMA)	Jul-10, May-11, Aug-11, Feb-12, May-12, Aug-12	Discharge, Heathcote, Heron
Ulva lactuca	Dec-09, Feb-10, Apr-10, Jul-10, Sep-10, Feb-11, May-11, Jul-11, Oct-11, Jan-12, Apr-12, Jul-12	Heron, Humphreys
Gracilaria chilensis	Dec-09, Apr-10, Jul-10, Jan-11, Oct-11, Jan-12	Heron, Humphreys
Zostera muelleri	Jan-11, Oct-11, Jan-12, Apr-12, Jul-12	Heron

4.2.2. Sample collection and treatment

Amphibola crenata, *Austrovenus stutchburyi*, *Austrohelice crassa*, *Macrophthalmus hirtipes*, *Hemigrapsus crenulatus, Diloma subrostrata, Microlenchus tenebrosus*, *Cominella glandiformis* and polychaetes were collected individually by hand. The smaller invertebrates (*Diloma*, *Microlenchus*, *Cominella* and polychaetes) were analysed intact, and so were held alive in filtered seawater for 48h after collection to allow the evacuation of gut contents. Fish (*Aldrichetta forsteri* (Yellow-eye mullet), *Rhombosolea plebeian* (Sand flounder), *Retropinna retropinna* (Common smelt)) were collected using hand-held seine nets deployed for approximately 10min at each site. All samples were held on ice following collection and stored at -20°C until analysis. Muscle tissue was then dissected from each of the large invertebrates (*Amphibola*, *Austrovenus*, *Austrohelice*, *Macrophthalmus* and *Hemigrapsus*) and fish species, dried at 60°C for 2-3d and ground to a fine powder using a mortar and pestle. For *Diloma*, *Microlenchus* and *Cominella*, whole animals were removed from their shells before being dried and ground. Polychaetes were processed whole.

Benthic microalgae (BMA) were scraped from the surface sediment using a scalpel blade, being careful to avoid as much sediment as possible. Scrapings were rinsed into a sterilised tube using deionised water. In the laboratory, the BMA sample was suspended in deionised water, allowing the heavier sediment to settle, which took from seconds to one minute. The suspension was then decanted into another

sterilised tube and the process continued until the suspension was free from sediment. The BMA suspension was placed into a centrifuge (10min at 3000rpm) and spun until a pallet formed. The pellet was dried at 60°C for 2-3d and ground to a fine powder.

Marine plants (*Ulva lactuca*, *Gracilaria chilensis* and *Zostera muelleri*) were collected by hand (where possible, attached specimens were collected) and stored at -20°C prior to processing. Plants were then washed with deionised water, removing any attached fauna, dried at 60°C for 2-3d and ground to a fine powder.

Pelagic particulate organic matter (POM) samples were collected from water samples that were filtered through pre-combusted GF/F filters (0.7µm retention) until filters were clogged with POM. Filters were then dried at 60°C for 2-3d. Following this, one drop of deionised water was added to each filter and filters were placed into a desiccator containing a beaker of 12M HCl for 8h to remove carbonates. Following acidification, samples were redried.

Sediment samples for benthic POM were collected from the top 2cm of the sediment surface and dried at 60°C for 2-3d. Samples were then placed into a desiccator containing a beaker of 12M HCl for 8h to remove carbonates. Following acidification, samples were redried and ground to a fine powder.

4.2.3. Earthquake impacts on estuarine sediment $\delta^{13}C$ and $\delta^{15}N$

To examine the impact of the 22 February 2011 earthquake on the isotopic composition of estuarine sediment, scrapings of surface (<2cm deep) sediment were collected from areas of old and new sediment (see *Chapter 3* for details of old and new sediments resulting from the earthquakes) at six sites (Avon, Discharge, Heathcote, Heron, Humphreys, Plover). These samples were collected 4-5 weeks after the event at Discharge, Humphreys and Heron, and 8-9 weeks after the event at Avon, Heathcote and Plover. The samples were processed as described in *4.2.2*.

4.2.4. Earthquake effects on consumer diets: translocation experiment

To test the effects of transplantation to sites with different conditions on the isotopic values of consumers, in November 2011*, Amphibola* and *Austrovenus* were taken from Discharge, and *Hemigrapsus* collected from Heron, and translocated to caged areas of old and new sediment at Humphreys and Heathcote. Cages were circular with a diameter of 15cm, a height of 40cm, and when inserted, resulted in 20cm of

cage protruding above the sediment surface and 20cm buried within the sediment. To prevent invertebrates from escaping, the cages included a bottom. Consequently, to insert the cage with minimal disruption to the vertical chemical and physical gradients present with the sediment, a sediment core, measuring the same height and diameter as the cage, was used to remove an intact portion of sediment. This intact sediment was then carefully placed within the cage and the cage + sediment was inserted into the area where the core had been removed. Once inserted, cages were left to consolidate for four weeks before adding the invertebrates. Invertebrates were left for 10 weeks before being collected (N=3 per treatment) and returned to the laboratory, where they were frozen at -20°C prior to processing. Muscle tissue was then dissected from each specimen, dried at 60°C for 2-3d and ground to a fine powder. Surface sediment samples were also collected from areas of old and new sediments at Humphreys and Heathcote at the completion of the translocation period in January 2011. Sediments were acidified to remove carbonates, dried at 60°C for 2-3d and ground to a fine powder.

4.2.5. Analysis of $\delta^{13}C$ and $\delta^{15}N$

Sub-samples of ~1mg for invertebrates, ~2mg for marine plants/microalgae and ~60mg for sediment, as well as whole filters containing POM, were analysed for $\delta^{13}C$ and $\delta^{15}N$. Individual samples of polychaetes and *Microlenchus* did not provide sufficient quantities of material for an analysis of replicate samples. Therefore, individuals were pooled to provide an integrated population estimate of natural stable isotope abundance. A small number of initial samples from December 2009 and early 2010 were sent to Waikato Stable Isotope Unit for analysis of $\delta^{13}C$ and $\delta^{15}N$ on an automated Europa Scientific 20/20 isotope analyser. This instrument combusted samples, separated the resulting gases by gas chromatography and then analysed them using continuous-flow mass spectrometry. All other samples were sent to University of California (UC) Davis Stable Isotope Facility where the glass fibre filters and sediments were analysed using an Elementar Vario EL Cube or Micro Cube elemental analyser (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The remaining samples (invertebrates, marine plants) were analysed using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Comparisons of

split samples analysed at both the Waikato Stable Isotope Unit and UC Davis Stable Isotope Facility showed a high level of agreement in $\delta^{13}C$ and $\delta^{15}N$ values between the two facilities (R^2>0.98 for both isotopes; Fig. 4.1).

Results are expressed in standard delta notations, where, for example, $\delta^{13}C = [(R_{sample}/R_{std})-1] \times 1000$ where $R_{sample} = {}^{13}C^{12}C$ of Peedee belemnite limestone. R_{std} for $\delta^{15}N$ was atmospheric nitrogen.

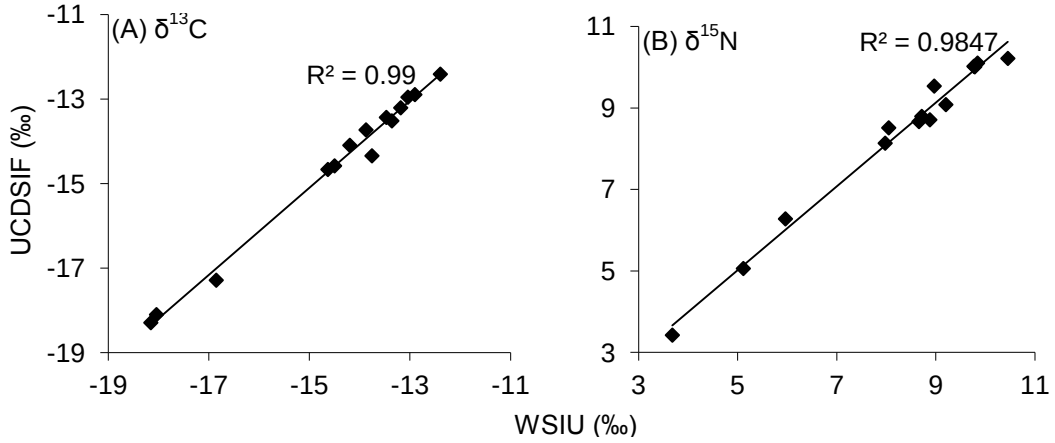

Figure 4.1. Comparison of $\delta^{13}C$ (A) and $\delta^{15}N$ (B) values from samples analysed at both University of California Davis Stable Isotope Facility (UCDSIF) and Waikato Stable Isotope Unit (WSIU). N=14.

4.2.6. Statistical analysis and interpretation of stable isotope results

General linear models (GLMs) were used to examine the effects of site (fixed), sampling period (three levels: pre-diversion, post-diversion/pre-earthquake, post-earthquake (fixed)) and dates nested within sampling periods (random) on the $\delta^{13}C$ and $\delta^{15}N$ values of each food source and consumer. Site was considered a fixed factor as each site represented a point on a eutrophication gradient.

For the experimental aspect, a one-way GLM was applied to test whether the translocated individuals (*Amphibola*, *Austrovenus* and *Hemigrapsus*) had isotopic values that differed from those at their source location at the start and end of the translocation period. Two models were run, one for $\delta^{13}C$ and the other for $\delta^{15}N$. Each model had six fixed factors: the $\delta^{13}C/\delta^{15}N$ values of individuals translocated to 1) old sediments at Heathcote, 2) new sediments at Heathcote, 3) old sediments at Humphreys, 4) new sediments at Humphreys, and the $\delta^{13}C/\delta^{15}N$ values of individuals at the source population at: 5) the start of the translocation period, and 6) the end of the translocation period. To test for differences in the isotopic values of the old and new sediments at Heathcote and Humphreys in January 2012, at the end

of the translocation period, a two-way GLM analysis with two factors: sediment type (fixed; 2 levels: old and new sediment) and site (fixed; 2 levels: Heathcote and Humphreys) was applied.

Where necessary, data were log-transformed to fulfil the assumptions of the model and where Cochran's test for homogeneity of variances remained significant following data transformation, p-values were made more conservative by reducing the significance threshold from 0.05 to 0.01 (Underwood 1997). Tukey post-hoc tests were done to examine the direction of significant relationships.

Dietary shifts of macrobenthos were assessed based on the visual observation of $\delta^{13}C$ versus $\delta^{15}N$ biplots. Mixing models (Phillips and Gregg 2001) were not used in the present study as the stable isotopic values of some benthic macrobenthos were out of the ranges of the values for potential organic matter sources. This was likely due to the large spatial and temporal scales examined and the fact that food sources and consumers were not always sampled at the same sites or on the same temporal regime (see Sakamaki and Richardson 2009). Trophic fractionation was considered to be 1‰ and 3‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively, in the assessment of stable isotope results for macrobenthos (DeNiro 1978, Middelburg and Levin 2009).

4.3. Results

4.3.1. $\delta^{13}C$ and $\delta^{15}N$ of primary producers and POM

The $\delta^{13}C$ values of BMA showed a significant site x date(sampling period) interaction effect across the three sampled sites, three sampling periods (pre-diversion, post-diversion/pre-earthquake and post-earthquake) and various dates within these periods. There were no significant effects of site or sampling period (Table 4.2). Values ranged between -12.48 to -20.86‰ (Fig. 4.2A). There was some suggestion of trends at particular sites, but these varied among sites. For example, Discharge started with low values before the earthquakes, rose slightly after this period, but had an almost identical value at the last period. Heron values fluctuated throughout the sampling and rose during the last period. Heathcote, however, began high and decreased almost linearly through time.

Table 4.2. General linear model analysis showing effects of site, sampling period (pre-diversion, post-diversion/pre-EQ, post-EQ), the interaction between site and sampling period, date (nested within sampling period) and the interaction between site and date(nested within sampling period) on the $\delta^{13}C$ (A) and $\delta^{15}N$ (B) values of food sources and consumers. For *Cominella*, *Diloma* and *Zostera* there is no test for site as samples were collected from only one site. BMA = benthic microalgae, *Gracilaria* = *Gracilaria chilensis*, *Ulva* = *Ulva lactuca, Zostera* = *Zostera muelleri*, *Amphibola* = *Amphibola crenata*, *Austrovenus* = *Austrovenus stutchburyi*, *Austrohelice* = *Austrohelice crassa*, *Hemigrapsus* = *Hemigrapsus crenulatus*, *Macrophthalums* = *Macrophthalmus hirtipes*, *Cominella* = *Cominella glandiformis*, *Diloma* = *Diloma subrostrata*, *Retropinna* = *Retropinna retropinna, Aldrichetta* = *Aldrichetta forsteri*, *Rhombosolea* = *Rhombosolea leporine*. *Cochran's test for homogeneity of variances still significant following data transformation, p-value reduced to 0.01.

(A) $\delta^{13}C$		**Site**			**Sampling Period**			**Site*Sampling Period**			**Date(Sampling Period)**			**Site*Date(Sampling Period)**		
		DF	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**
Sources	BMA	2	0.68	0.54	1	0.48	0.51	1	0.020	0.59	4	0.76	0.58	6	42.10	**<0.001**
	Gracilaria[1]				2	1.72	0.20									
	Gracilaria[2]	1	5.54	**0.028**												
	Ulva	2	1.39	0.32	2	2.47	0.14	2	0.29	0.76	9	2.08	0.19	6	12.07	**<0.001**
	Zostera				1	0.35	0.56									
	Sediment POM	4	28.61	**<0.001**	2	0.47	0.64	7	4.23	**0.0025**	8	3.15	**0.010**	30	5.52	**<0.001**
	Pelagic POM	3	139.89	**<0.001**	2	2.16	0.19	5	8.33	**0.0011**	7	3.32	**0.033**	12	13.91	**<0.001**
Consumers	*Amphibola*	5	101.98	**<0.001**	2	12.83	**0.0016**	8	11.06	**<0.001**	9	0.94	0.51	34	1.26	0.18
	Austrovenus	4	83.99	**<0.001**	2	8.47	**0.0067**	8	10.63	**<0.001**	9	1.96	0.079	31	3.01	**<0.001**
	Austrohelice	1	1.31	0.32	2	2.05	0.17	1	0.031	0.87	8	0.53	0.80	4	2.90	0.037*
	Hemigrapsus	1	6.54	0.048*	2	2.73	0.16	2	2.46	0.18	6	0.37	0.87	5	2.87	0.027*
	Macrophthalmus	3	3.58	0.038*	2	0.42	0.66	2	9.04	**0.0027**	8	2.29	0.077	16	2.4	**0.006**
	Cominella				1	0.45	0.54									
	Diloma				1	0.75	0.43									
	Retropinna	1	0.036	0.88	1	0.096	0.81	1	2.59	0.15						
	Aldrichetta	5	3.31	0.11	1	0.27	0.63	5	6.60	**0.0005**						
	Rhombosolea	2	7.24	0.12	1	0.12	0.77	2	0.54	0.60						

(B) $\delta^{15}N$		**Site**			**Sampling Period**			**Site*Sampling Period**			**Date(Sampling Period)**			**Site*Date(Sampling Period)**		
		DF	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**	**DF**	**F**	**p**
Sources	BMA	2	3.83	0.084	1	1.03	0.35	1	0.51	0.50	4	1.03	0.46	6	2.58	0.041*
	Gracilaria[1]				2	10.16	**<0.001**									
	Gracilaria[2]	1	0.18	0.67												
	Ulva	2	1.35	0.33	2	3.97	0.057	2	0.87	0.47	9	7.03	0.016*	6	2.51	0.034*
	Zostera				1	11.57	0.0047*									
	Sediment POM	4	1.29	0.30	2	0.22	0.81	7	3.66	**0.0060**	8	0.86	0.56	30	2.65	**<0.001**
	Pelagic POM	3	3.99	0.034*	2	3.37	0.11	5	2.81	0.066	7	1.08	0.43	12	52.46	**<0.001**
Consumers	*Amphibola*	5	118.09	**<0.001**	2	2.67	0.12	8	2.25	0.047*	9	1.08	0.40	34	1.50	0.058
	Austrovenus	4	117.52	**<0.001**	2	4.38	0.040*	8	2.99	0.014*	9	1.19	0.34	31	1.31	0.16
	Austrohelice	1	0.01	0.92	2	1.72	0.23	1	5.42	0.11	8	5.42	0.072	4	0.55	0.70
	Hemigrapsus	1	0	0.96	2	9.22	0.016*	2	1.42	0.32	6	0.79	0.61	5	1.49	0.22
	Macrophthalmus	3	35.76	**<0.001**	2	4.16	0.046*	2	2.05	0.17	8	4.33	**0.0068**	16	1.44	0.15
	Cominella				1	0.31	0.61									
	Diloma				1	9.61	**0.036**									
	Retropinna	1	0.3	0.69	1	0.01	0.95	1	0.93	0.36						
	Aldrichetta	5	4.57	0.060	1	1.51	0.27	5	1.38	0.27						
	Rhombosolea	2	1.08	0.48	1	6.41	0.13	2	9.00	**0.0041**						

[1]Analysis of Humphreys site only

[2]Analysis of Humphreys and Heron sties during the post-diversion/pre-earthquake period only

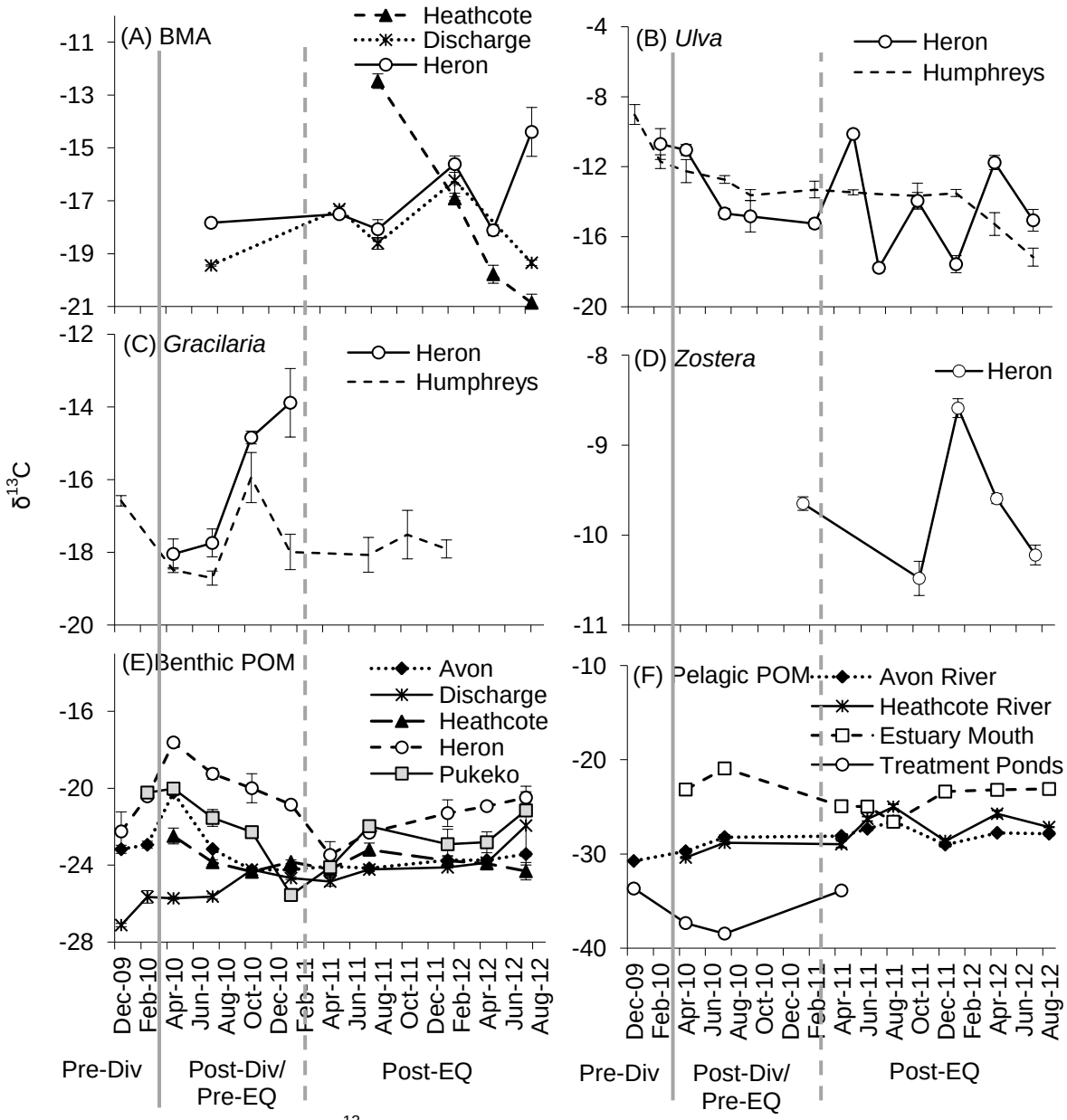

Figure 4.2. Average (±SE) $\delta^{13}C$ values of benthic microalgae (BMA) (A), *Ulva lactuca* (B), *Gracilaria chilensis* (C), *Zostera muelleri* (D), benthic POM (E) and pelagic POM (F) at various sites on dates between December 2009 and August 2012 spanning three sampling periods: pre-diversion, post-diversion/pre-earthquake and post-earthquake. N=3-4. Solid grey line indicates the timing of the diversion and the dashed grey line indicates the timing of the February 2011 earthquake.

As for BMA, *Ulva* values showed a significant site x date(sampling period) interaction effect but the site effect was not significant (Table 4.2A). There was a decline at Humphreys over time, as $\delta^{13}C$ values became more depleted (Fig. 4.2B). Heron values were far more variable between sampling dates than those at Humphreys, particularly from March 2011 to June 2012.

Gracilaria was problematical in analysing through time because it was found in only small abundances at Heron in the early part of the study, and not at all at this

site from June 2011 onwards. The two sites were significantly different in the year after the diversion and before the February 2011 earthquake (Table 4.2A; Fig. 4.2C). Values of $\delta^{13}C$ were more depleted at Humphreys than Heron. Post-diversion values at Humphreys were mostly smaller than those in the initial sampling period. Of particular note were the sharp peaks in values at both sites in October 2010 after the diversion but before the February 2011 earthquakes.

Zostera came into only one site, Heron, after the diversion (Fig. 4.2D). The different times of sampling had greatly different average values, ranging from -8.59 to -10.48‰, with a big spike in January 2012, a period when BMA values also increased.

Particulate organic matter (POM), both sediment and pelagic forms, had the most depleted $\delta^{13}C$ values found for any food source. Values of $\delta^{13}C$ for sediment POM were variable among sites and showed significant effects of site, site x sampling period, date(sampling period) and site x date(sampling period) (Table 4.2A). At Discharge, sediment POM was the most depleted but increased over time (Fig. 4.2E). The most enriched values were found in sediments at Heron and Pukeko. Peaks occurred in April 2010 immediately after the diversion at Avon and Heron, and at these sites, as well as Pukeko, there was a reduction in $\delta^{13}C$ values between April 2010 and early 2011. Sediments at Heathcote showed the least variation over time.

Pelagic POM had $\delta^{13}C$ values that differed significantly among sites and there was a significant site x date(sampling period) interaction effect (Table 4.2A). Samples taken from the treatment ponds had the most depleted $\delta^{13}C$ values, all of which were <-33‰ (Fig. 4.2F). Both the Avon and Heathcote rivers had values that were around -28‰ throughout the sampling periods. Oceanic POM (collected at the estuary mouth) was more enriched, with $\delta^{13}C$ values ranging from -20.92 to -26.58‰ over time.

The $\delta^{15}N$ values of primary producers and POM showed some interesting contrasts with the $\delta^{13}C$ values over sites and times. BMA values ranged from 1.02 to 7.15‰ (Fig. 4.3B) but did not vary significantly among sites or sampling periods (Table 4.2B). They were, however, most depleted at Discharge, and similar at the other two sites, Heathcote and Heron (Fig. 4.3A). Within sites, values were relatively constant over time but the final values at Discharge showed there may have been an improvement as BMA values moved towards those found at Heathcote and Heron.

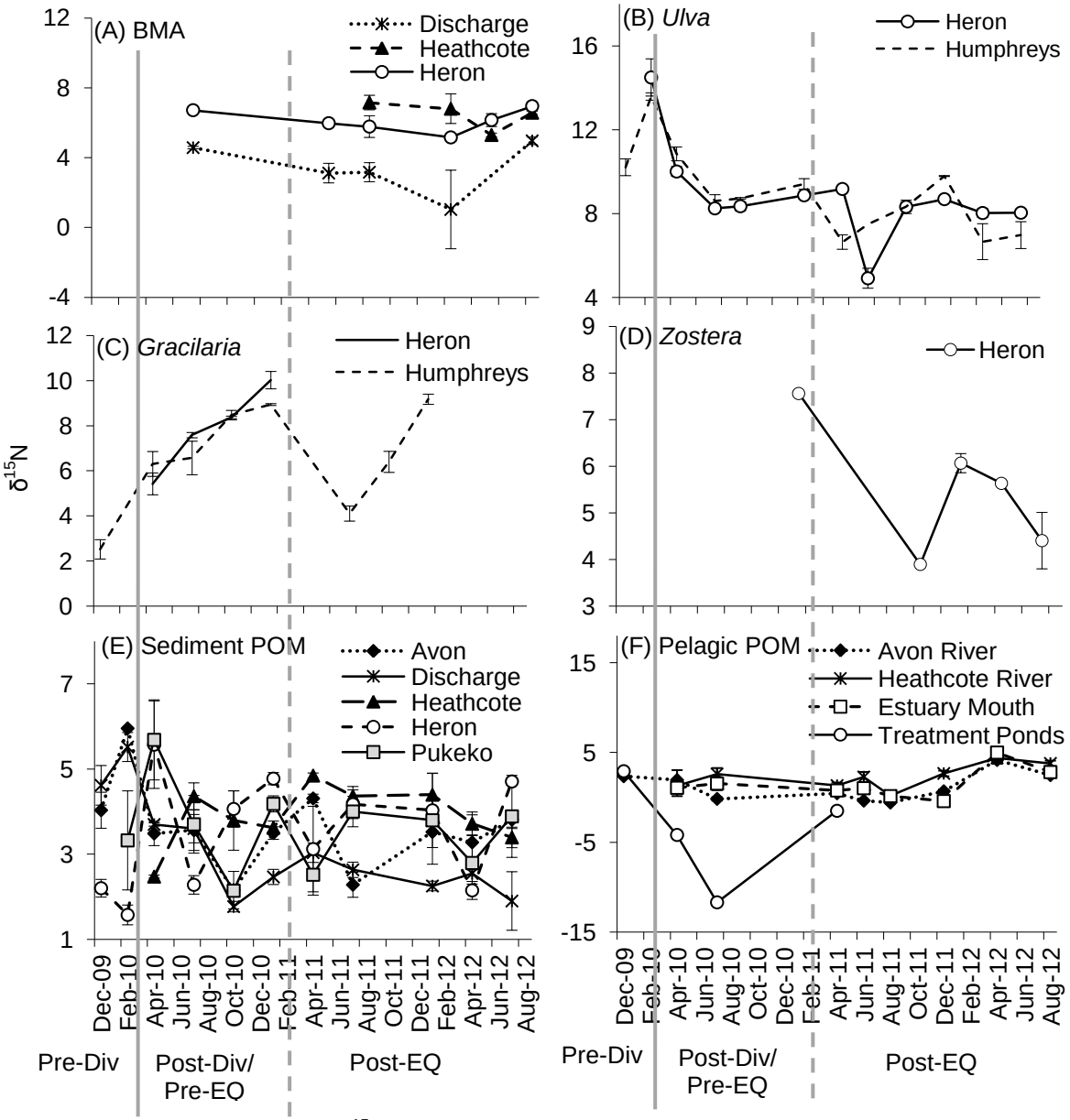

Figure 4.3. Average (±SE) $\delta^{15}N$ values of benthic microalgae (BMA) (A), *Ulva lactuca* (B), *Gracilaria chilensis* (C), *Zostera muelleri* (D), benthic POM (E) and pelagic POM (end-members) (F) at various sites on dates between December 2009 and August 2012 spanning three sampling periods: pre-diversion, post-diversion/pre-earthquake and post-earthquake. N=3-4. Solid grey line indicates the timing of the diversion and the dashed grey line indicates the timing of the February 2011 earthquake.

There were no significant effects of site or sampling period on the $\delta^{15}N$ values of *Ulva* (Table 4.2B). Despite this, values at both sites peaked in April 2010 and decreased to remain fairly consistent from June 2010 to June 2012. This is with the exception of relatively depleted values that occurred in June 2011, indicating the effects that the earthquakes, in particular the input of raw sewage, may have had on the nitrogen isotopic composition of this species (Fig. 4.3B).

Similar to *Ulva*, $\delta^{15}N$ values of *Gracilaria* did not differ significantly between sites during the post-diversion/pre-earthquake period, when the only site comparison could be made (Table 2B). *Gracilaria* at Humphreys showed a significant change over time with $\delta^{15}N$ values increasing between December 2009 and January 2011 and decreasing immediately after the earthquake, again probably reflecting the uptake of raw sewage. There was some recovery to pre-earthquake values from July 2011 onwards (Table 2B, Fig. 4.3C).

There was a significant change in the $\delta^{15}N$ values of *Zostera* over time (Table 2B). The highest value occurred pre-earthquake in December 2010 and there was a large reduction after the earthquake. Values peaked again in December 2011 but were not as high as values in December 2010 (Fig. 4.3D). There was a trend of lower values in the winter months.

There were significant site x sampling period and site x date(sampling period) interaction effects for the $\delta^{15}N$ values of sediment POM (Table 4.2B). Values at all sites showed temporal fluctuation around a central value, generally 3-4‰ but displayed no clear trend (Fig. 4.3E). Overall values at Discharge were generally more depleted than at the other sites.

The $\delta^{15}N$ values of pelagic POM also showed a significant site x date(sampling period) interaction effect (Table 2B). Values were similar at the river sites and the ocean but more depleted at the treatment ponds (Fig. 4.3F). At the treatment ponds, there was substantial fluctuation, with a reduction in values between December 2009 and July 2010, and an increase between July 2010 and April 2011. With the exception of the treatment ponds, $\delta^{15}N$ values of pelagic POM at the other sites were largely consistent over time.

The immediate effects of the earthquakes on isotopic values were apparent in the old and new (liquefaction-derived) sediments. New sediment isotopic ratios across sites were tightly clustered at low (light) ratios of both elements whereas old sediment ratios were more widely distributed, for both elements, with heavier ratios (Fig. 4.4). In general, values in the upper right of graphs (with higher values of both isotopes) are characteristic of those associated with organic-rich sediments affected by pollution and/or a higher accumulation of marine-derived organic matter. Those in the lower left quadrant are often more characteristic of more pristine sediments usually of a more terrestrial origin. Note in particular the exceptionally low values of $\delta^{13}C$ (around -24‰). General linear models showed that $\delta^{13}C$ values were

significantly different among sites ($F_{5,24}$=18.23 p<0.001), sediment types ($F_{1,24}$=42.57 p<0.001), and the interaction effect was significant ($F_{5,24}$=3.41 p=0.018). There was greater among site spatial variability in values of old sediments. In assessing the two isotopes separately, there were no significant differences in $\delta^{15}N$ values among sites ($F_{5,24}$=1.27 p=0.31), but significant differences between sediment types ($F_{1,24}$= 18.58 p=0.0002), with a NS interaction ($F_{5,24}$=0.53 p=0.75). New sediments at Plover and old sediments at Humphreys had the lowest and highest $\delta^{15}N$ values respectively (Fig. 4.4). The relatively high $\delta^{13}C$ values of old sediments at Plover and Humphreys indicated a higher proportion of marine-derived organic matter such as algae and/or seagrass being incorporated into the sediment as detritus.

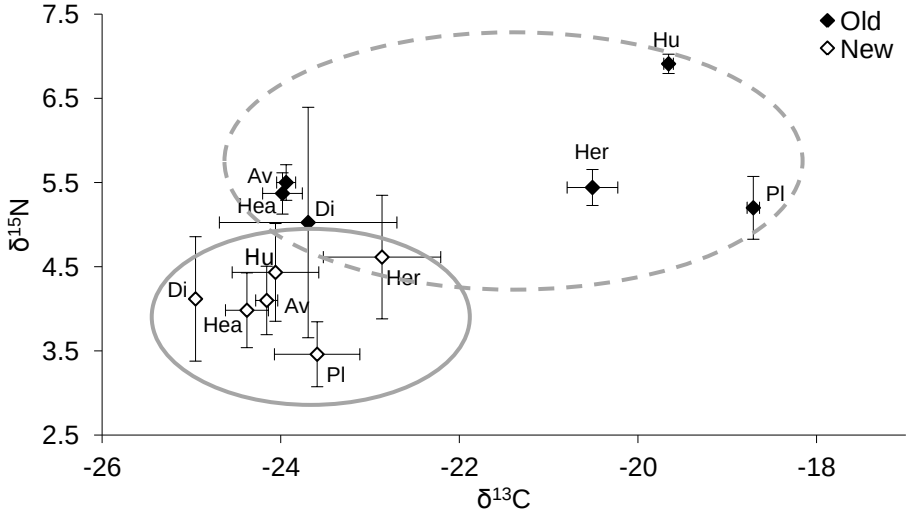

Figure 4.4. Average (±SE) $\delta^{13}C$ and $\delta^{15}N$ values of surface (<2cm depth) sediment collected from old and new sediments produced by the February 2011 earthquake at six sites: Avon (Av), Discharge (Di), Heathcote (Hea), Heron (Her), Humphreys (Hu) and Plover (Pl) 31-70 days (site dependent) after the February 2011 earthquake. The dashed grey line encompasses the old sediments from all sites and the solid grey line encompasses the new sediments from all sites. N=3.

4.3.2. $\delta^{13}C$ and $\delta^{15}N$ of consumers

The individual isotopic signatures for consumers at most sites were quite variable through time. There were significant effects of site, sampling period and the interaction term on the $\delta^{13}C$ values of *Austrovenus* and *Amphibola* (Table 2A). For both species, values were most depleted at Discharge and most enriched at sites closest to the estuary mouth (Heron and Plover). The riverine sites (Avon and Heathcote) showed intermediate values (Fig. 4.5A&B). Values at Discharge increased over time, particularly for *Austrovenus*, becoming more similar to the other

sites. At the other sites however, there were no clear patterns of change through time and Pukeko, in particular, showed little temporal variation.

Austrohelice had $\delta^{13}C$ values that were slightly enriched at Pukeko relative to Avon but no clear temporal trends were apparent at either site (Fig. 4.5C). *Hemigrapsus* at Discharge and Heron had low and high $\delta^{13}C$ values respectively prior to the diversion (Fig. 4.5D). Their values became more similar after the diversion, converging in October 2010 and following the same trajectory of change thereafter. Values increased from December 2011 onwards. *Macrophthalmus* was the only crab species to show any significant effects, with significant site x sampling period and site x date(sampling period) interactions (Table 2A). Here, $\delta^{13}C$ values increased over time from -17.36 in October 2010 to -10.77 in June 2012 (Fig. 4.5E). Values at the other sites were more similar over space and time.

Polychaetes at Discharge showed no change in $\delta^{13}C$ values between January 2011 and January 2012 (Fig. 4.6A). *Nicon* sampled at Avon decreased whereas the $\delta^{13}C$ value of Orbinidae became more enriched over this 12 month period. The $\delta^{13}C$ values of *Diloma* and *Microlenchus* showed a trend (although not significant; Table 4.2A) of becoming more depleted between January 2011 and January 2012 (Fig. 4.6B&C). In contrast, *Cominella* did not change over this period (Fig. 4.6D; Table 4.2A).

No significant spatial or temporal changes were found for the $\delta^{13}C$ values of *Retropinna* (Table 4.2A). There was, however, a significant site x sampling period interaction effect for *Aldrichetta* (Table 4.2A). This species had $\delta^{13}C$ values that were enriched at Mt Pleasant, Ebbtide St and Pleasant Point relative to individuals sampled from Shag Rock, Tern St and the treatment ponds over both sampling periods. *Aldrichetta* sampled from the treatment ponds showed a large enrichment in $\delta^{13}C$ between January 2011 and January 2012 (Fig. 4.7B). There were no significant effects for *Rhombosolea* (Table 4.2A) but this species showed more enriched $\delta^{13}C$ values at Tern St, closer to the estuary mouth, than at Pleasant Point and Mt Pleasant, situated close to the Avon and Heathcote rivers respectively (Fig. 4.7C). No patterns of temporal change were seen for *Rhombosolea* at any site.

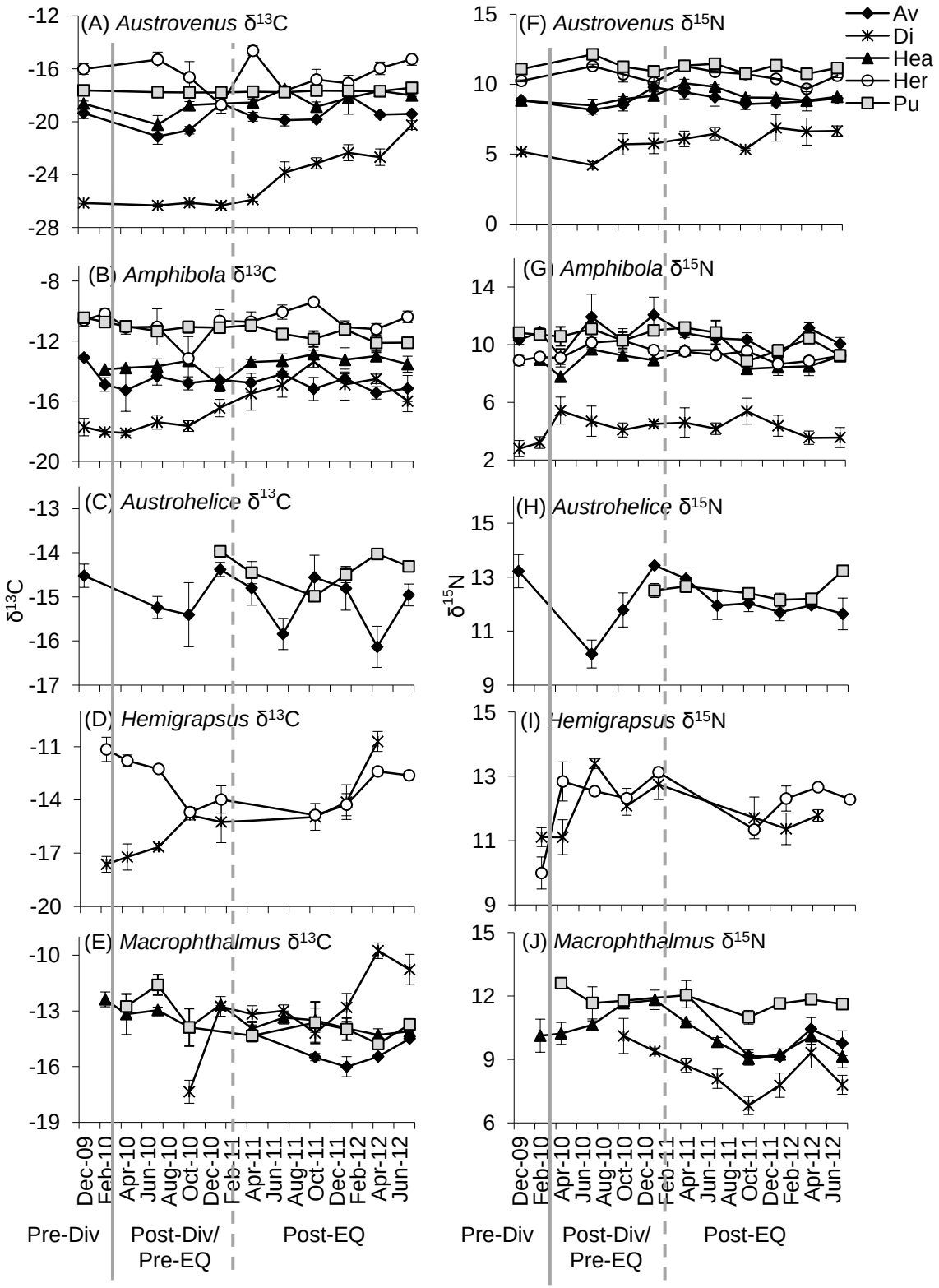

Figure 4.5. Average (±SE) $\delta^{13}C$ (A-E) and $\delta^{15}N$ (F-J) values of *Austrovenus stutchburyi* (A,F), *Amphibola crenata* (B,G), *Austrohelice crassa* (C,H), *Hemigrapsus crenulatus* (D,I) and *Macrophthalmus hirtipes* (E,J) on sampling occasions between December 2009 and July 2012 spanning three sampling periods (pre-diversion, post-diversion/pre-EQ and post-EQ) at five sites: Avon (Av), Discharge (Di), Heathcote (Hea), Heron (Her) and Pukeko (Pu). N=3. Solid grey line indicates the timing of the diversion and the dashed grey line indicates the timing of the February 2011 earthquake.

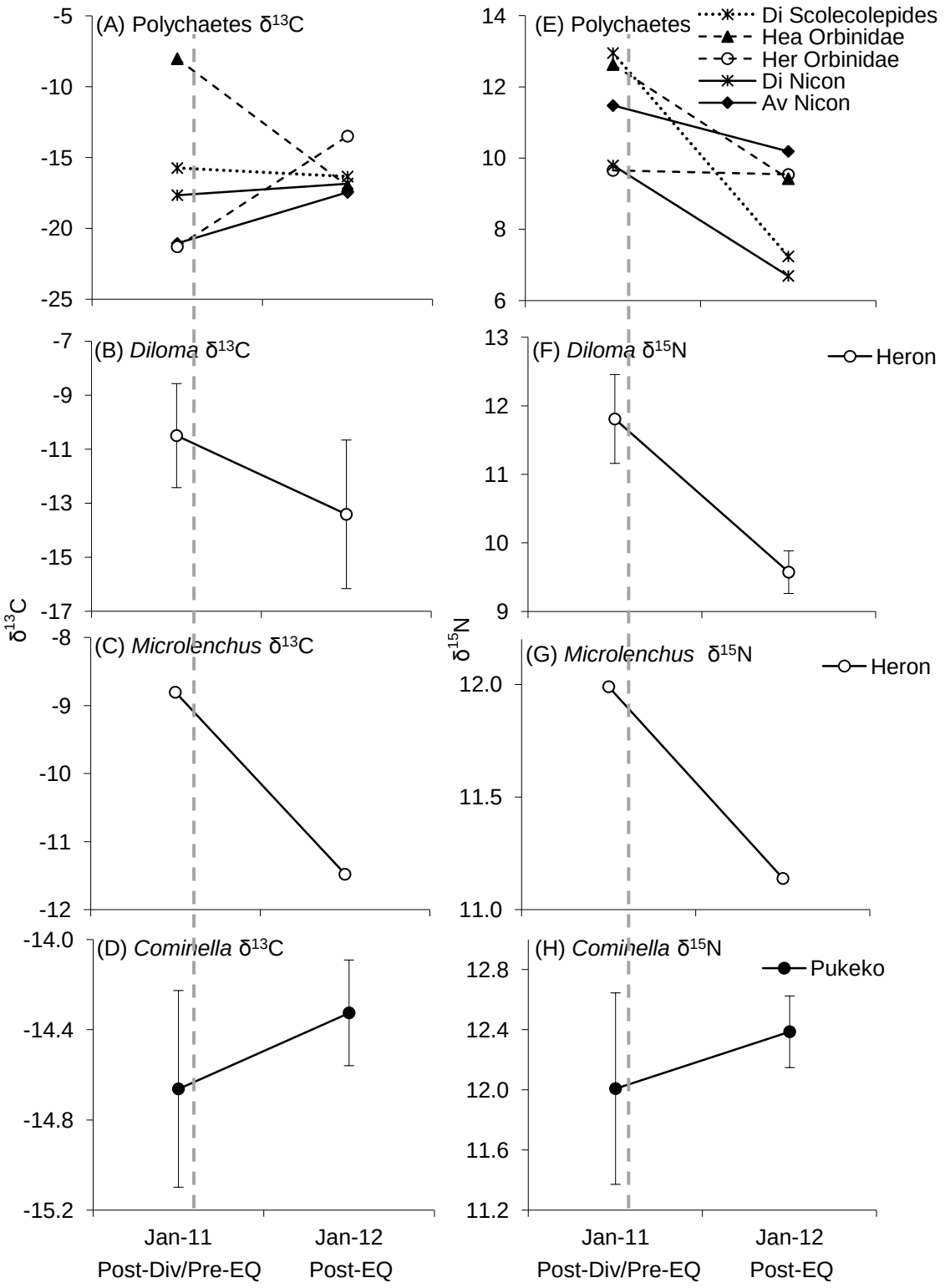

Figure 4.6. Average (±SE) $\delta^{13}C$ (A-D) and $\delta^{15}N$ (E-H) values of Polychaetes (A,E), *Diloma subrostrata* (B,F), *Microlenchus tenebrosus* (C,G) and *Cominella glandiformis* (D,H) sampled in January 2011 (post-diversion/pre-EQ) and January 2012 (post-EQ) at sites where they were present. For polychaetes and *Microlenchus* values represent a composite sample of multiple individuals. For *Cominella* and *Diloma* samples, each sample is a separate individual and N=3. For A,C,E and G one replicate of composite samples are plotted and hence there are no error bars. Di *Scolecolepides*=Discharge (site) *Scolecolepides benhami*, Hea Orbinidae=Heathcote Orbinidae, Di *Nicon*=Discharge *Nicon aestuariensis*, Av *Nicon*=Avon *Nicon aestuariensis*. The dashed grey line indicates the timing of the February 2011 earthquake.

The $\delta^{15}N$ values of *Amphibola* and *Austrovenus* varied significantly among sites (Table 2B). Similar to $\delta^{13}C$ values, $\delta^{15}N$ values for these species were most depleted at Discharge (Fig. 4.5F&G). *Austrovenus* was most enriched closest to the estuary mouth and the river sites had intermediate values. For *Amphibola,* values were similar among the riverine (Avon and Heathcote) and more oceanic (Heron and Pukeko) sites. The $\delta^{15}N$ values of *Austrovenus* at Discharge increased over time, becoming more enriched and more similar to this species at the other sites. *Amphibola* showed an initial enrichment in the nitrogen isotope, but there was then minimal change from April 2010 to June 2012.

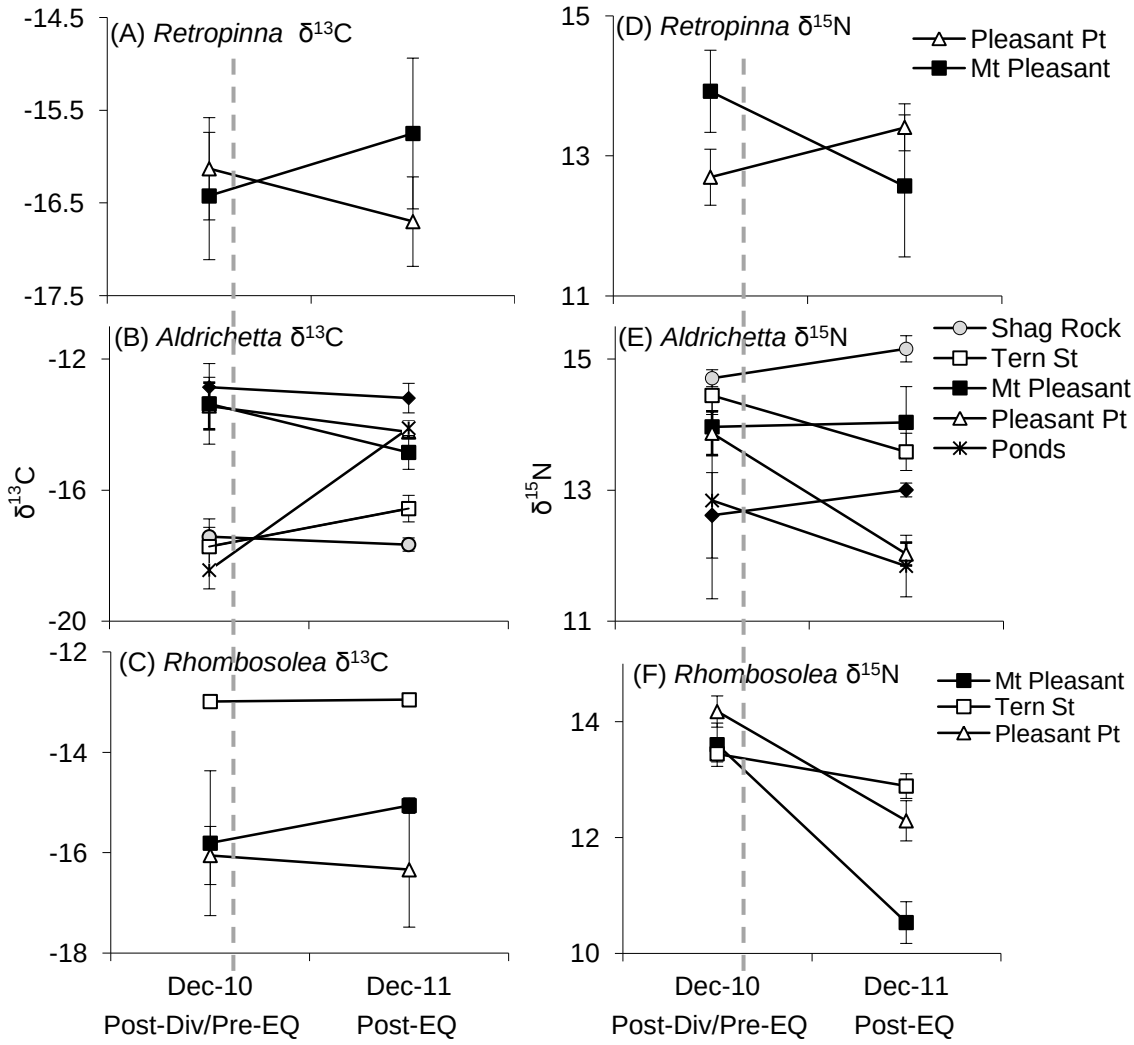

Figure 4.7. Average (±SE) $\delta^{13}C$ (A-C) and $\delta^{15}N$ (D-F) values for *Retropinna retropinna* (Common smelt) (A,D), *Aldrichetta forsteri (*Yellow-eyed mullet) (B,E) and *Rhombosolea leporina* (Yellowbelly flounder) (C,F) at various sampling locations in December 2010 and December 2011. N=3. The dashed grey line indicates the timing of the February 2011 earthquake.

There were no significant effects of site or sampling period on the $\delta^{15}N$ values of *Austrohelice* (Table 2B). With the exception of depleted values occurring at Avon in July 2010, there was little temporal variation for these crabs, particularly at Pukeko (Fig. 4.5H). Values at both sites were similar over time. *Hemigrapsus* had $\delta^{15}N$ values that were similar between sites and values at both sites increased between February 2010 and July 2010 although this was not significant (Table 2B; Fig. 4.5I). There was a significant effect of site on the $\delta^{15}N$ values of *Macrophthalmus* (Table 4.2B). Values for individuals of this species at Discharge were more depleted than for individuals at the other sites. At both Discharge and Heathcote, $\delta^{15}N$ values decreased between October 2010 and October 2011 (Fig 4.5J).

Polychaetes at all sites except Heron had more depleted values of $\delta^{15}N$ in January 2012 than in January 2011. This change was greatest for *Scolecolepides benhami* at Discharge. Orbinidae at Heron showed similar $\delta^{15}N$ values in 2011 and 2012 (Fig. 4.6E). There was a significant effect of sampling period on the $\delta^{15}N$ values of *Diloma* (Table 4.2B), reflecting a reduction in $\delta^{15}N$ values between 2011 and 2012 (Fig. 4.6F). *Microlenchus* showed a trend of becoming more depleted between January 2011 and January 2012 although there were no replicate samples to determine the significance of this (Fig 4.6G). There were no significant differences in the $\delta^{15}N$ values of *Cominella* between January 2011 and January 2012 (Table 2B; Fig. 4.6H). The $\delta^{15}N$ values of *Retropinna* did not show any significant changes between December 2010 and December 2011 at the two sites where this species was collected (Table 4.2B; Fig. 4.7D). Similarly, there were no significant changes in the $\delta^{15}N$ values of *Aldrichetta* (Table 2B). Individuals sampled in 2010 were, however, most enriched at Shag Rock and Tern St, sites nearest to the estuary mouth, and most depleted at the treatment ponds and Ebbtide St (Fig. 4.7E). The $\delta^{15}N$ values at Tern St, Pleasant Pt and the treatment ponds decreased over time, becoming relatively more depleted in 2011. The $\delta^{15}N$ values of *Rhombosolea* showed a significant site x sampling period effect (Table 4.2B). Individuals of this species were more enriched in 2010 than in 2011 at all sites (Fig. 4.7F). This difference was largest for *Rhombosolea* sampled at Mt Pleasant and lowest for individuals sampled at Tern St.

4.3.3. Trophic interactions

Trophic interactions were assessed based on the relative positioning of food sources and consumers on $\delta^{13}C$ versus $\delta^{15}N$ biplots. These plots showed that particulate organic matter and primary producers occupied the lowest trophic levels but there was considerable range (>8‰) in the $\delta^{15}N$ values of these basal food sources with pelagic POM < sediment POM < BMA < marine plants (Fig. 4.8). In general, the molluscan species (except *Cominella)* tended to occupy the first consumer trophic level/s and *Cominella*, crabs and fish occupied the higher trophic levels. The $\delta^{15}N$ values of *Diloma* and *Microlenchus* were enriched by approximately 3‰ relative to *Ulva* and they had similar $\delta^{13}C$ values. *Zostera* did not appear to contribute, in any significant quantity, to the diets of any of the consumers examined (Fig. 4.8). The positioning of *Gracilaria* relative to consumers indicated that it contributed significantly to the diets of *Amphibola, Austrovenus* and polychaetes; but, based on what is known about the diets of these species, this is unlikely. More likely is that the relationship between the isotopic signatures of these consumer species and *Gracilaria* is unrelated (Fig. 4.8). From the trophic positioning of the fish species, they are likely feeding on juvenile crabs and polychaetes, and possibly other small crustaceans that were not studied. *Ulva* appeared to contribute significantly to the diet of the crab species, with other marine plant taxa and BMA likely contributing smaller quantities.

The $\delta^{13}C$ versus $\delta^{15}N$ biplots of *Austrovenus* and *Amphibola* and their potential food sources supported that, at the river and oceanic sites, there was no change in the diets of these consumers over the three sampling periods (Fig. 4.9). Plots indicated that both *Amphibola* and *Austrovenus* were receiving a large portion of their diet from BMA (presumably resuspended for *Austrovenus*). For *Austrovenus* at Discharge, $\delta^{13}C$ values increased over time, likely reflecting a switch from a predominately sewage-derived POM/BMA diet, to a predominantly BMA/oceanic POM diet for these clams (Fig. 4.9). Based solely on the relative positioning of *Amphibola* and food sources, plots indicated that *Ulva*, *Gracilaria* and *Zostera* were contributing to *Amphibola* diet, likely as detritus, as well as BMA (Fig. 4.9).

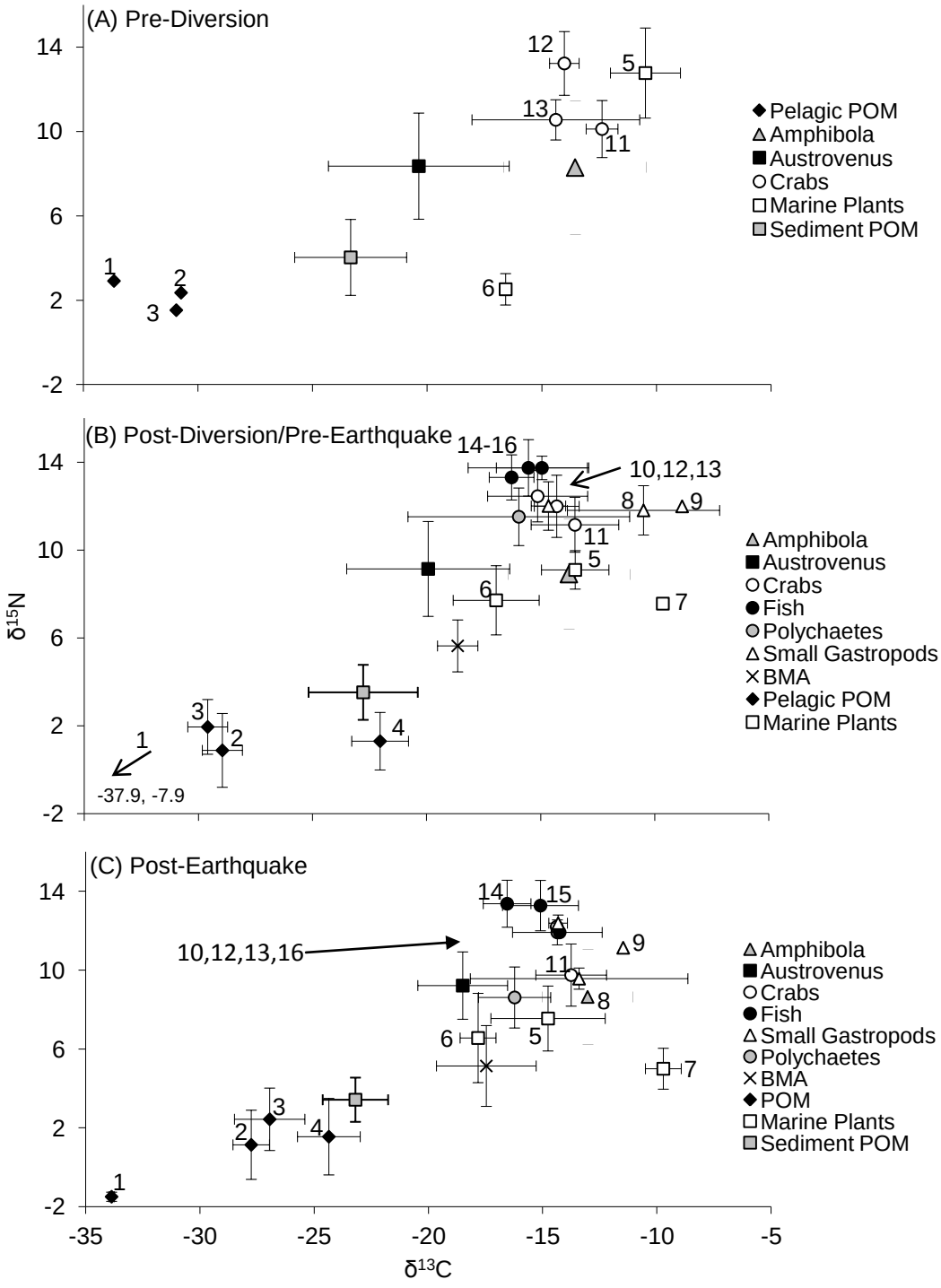

Figure 4.8. Average (±SD) $\delta^{13}C$ and $\delta^{15}N$ values of all primary producers, food sources and consumers sampled in the Avon-Heathcote Estuary on various occasions between December 2009 and August 2012. Plotted values represent average values for each food source/organism during the pre-diversion (A), post-diversion/pre-EQ (B) and post-EQ (C) periods, across all sites sampled. 1=sewage treatment pond POM, 2=Avon River POM, 3=Heathcote River POM, 4=estuary mouth POM, 5=*Ulva lactuca*, 6=*Gracilaria chilensis*, 7=*Zostera muelleri*, 8=*Diloma subrostrata*, 9=*Microlenchus tenebrosus*, 10=*Cominella glandiformis*, 11=*Macrophthalmus hirtipes,* 12=*Austrohelice crassa*, 13=*Hemigrapsus crenulatus*, 14=*Retropinna retropinna*, 15=*Aldrichetta forsteri*, 16=*Rhombosolea leporine.*

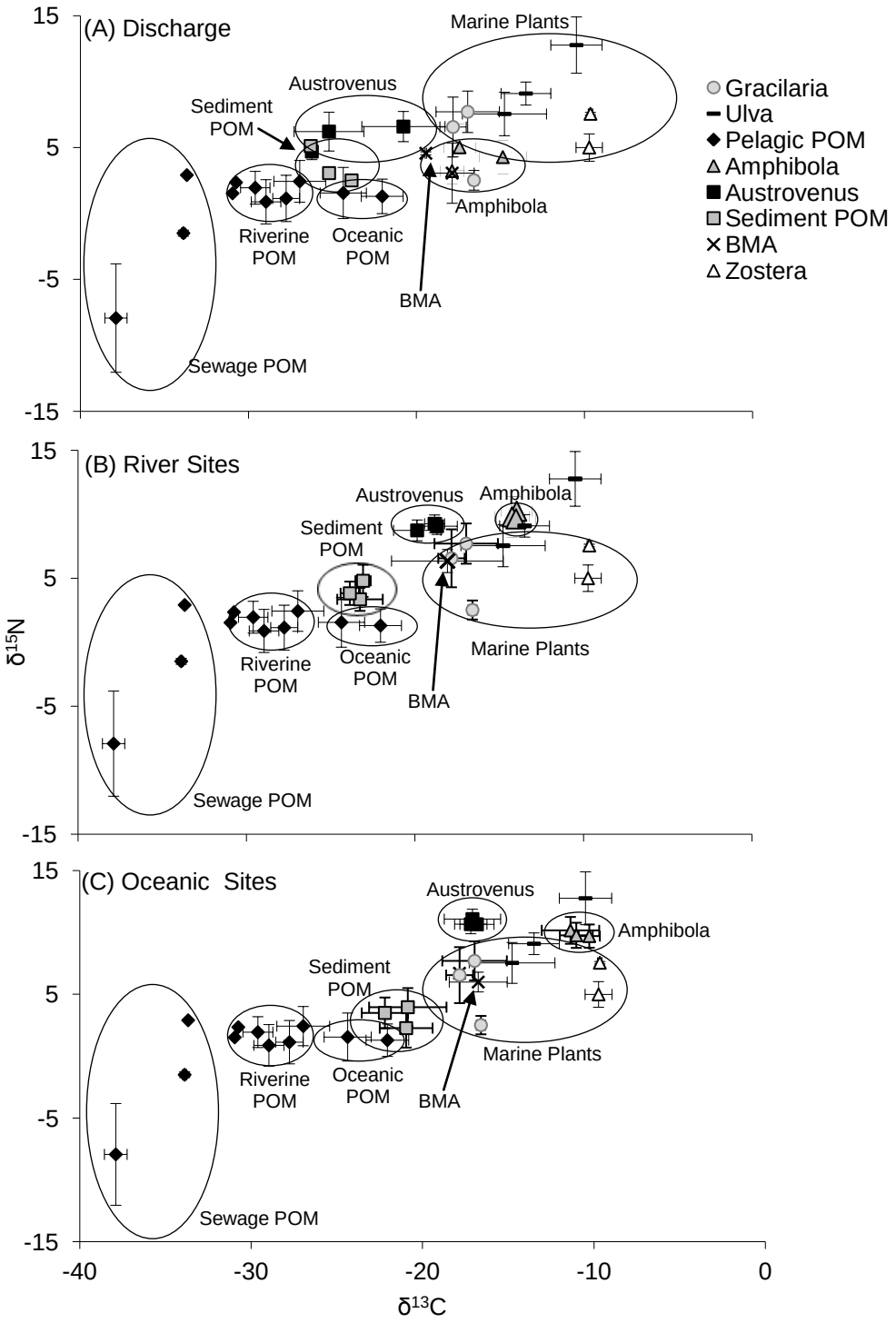

Figure 4.9. Average (±SD) $\delta^{13}C$ and $\delta^{15}N$ values of all primary producers and *Austrovenus stutchburyi* and *Amphibola crenata* sampled in the Avon-Heathcote Estuary on various occasions between December 2009 and August 2012 at the Discharge site (A), the riverine sites (Avon and Heathcote) (B) and the oceanic sites (Heron and Pukeko) (C). Where data is available, there are three data points plotted for each food source/consumer for each set of sites, with each data point representing the average (±SD) value for each of the three time periods (pre-diversion, post-diversion/pre-EQ and post-EQ). Ovals indicate the region where most $\delta^{13}C$ and $\delta^{15}N$ values for each of the food sources and consumers at (A), (B) and (C) are located.

Figure 4.10 shows that the range of $\delta^{13}C$ values for benthic POM overlaps with those for BMA, *Gracilaria* and *Ulva*, indicating the likely contribution of each of these components to sediment POM. The range of $\delta^{13}C$ values for old sediment is greater than that for new sediment, overlapping with BMA, *Ulva* and *Gracilaria* indicating a contribution of these to old sediment POM. The range of new sediment values, however, do not overlap with any of these marine-derived organic matter components (Fig. 4.11).

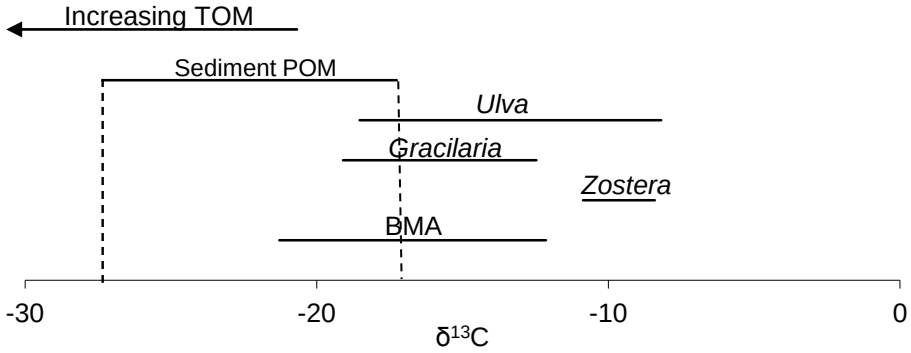

Figure 4.10. Range of $\delta^{13}C$ values of sediment POM and its potential constituents: BMA, *Gracilaria chilensis*, *Ulva lactuca* and *Zostera muelleri*. The plotted range is calculated from values across all sites and time periods. Dashed lines show the region where potential contributors to sediment POM are expected to lie. TOM = terrestrially-derived organic matter.

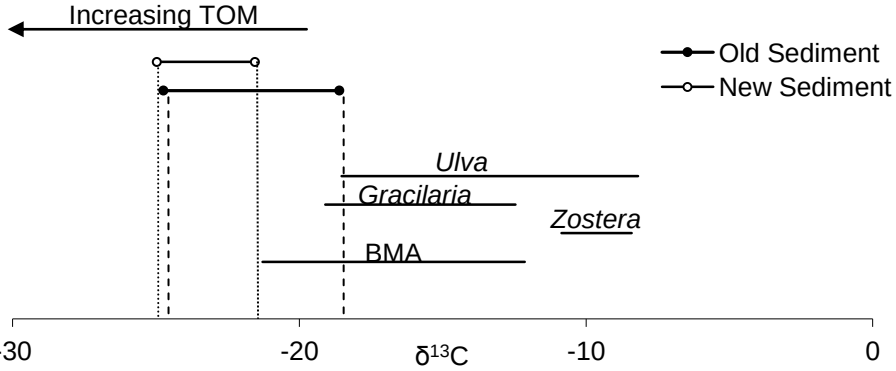

Figure 4.11. Range of $\delta^{13}C$ values of old and new sediment POM at Humphreys and Heathcote 31-70 days after the February 2011 earthquake. For comparison purposes, the range in $\delta^{13}C$ values of its potential constituents: BMA, *Gracilaria chilensis*, *Ulva lactuca* and *Zostera muelleri*, are plotted. These are calculated from values across all sites and time periods. Dotted and dashed lines indicate the regions where potential contributors to new sediment and old sediment POM, respectively, are expected to lie. TOM = terrestrially-derived organic matter.

The range of $\delta^{13}C$ values for oceanic pelagic POM overlap with those of marine plankton, sediment POM and BMA, indicating a contribution of these components to oceanic POM (Fig. 4.12). Riverine POM and, especially, sewage ponds POM, had more negative $\delta^{13}C$ values, indicating a higher contribution of terrestrially (including sewage-derived) organic matter.

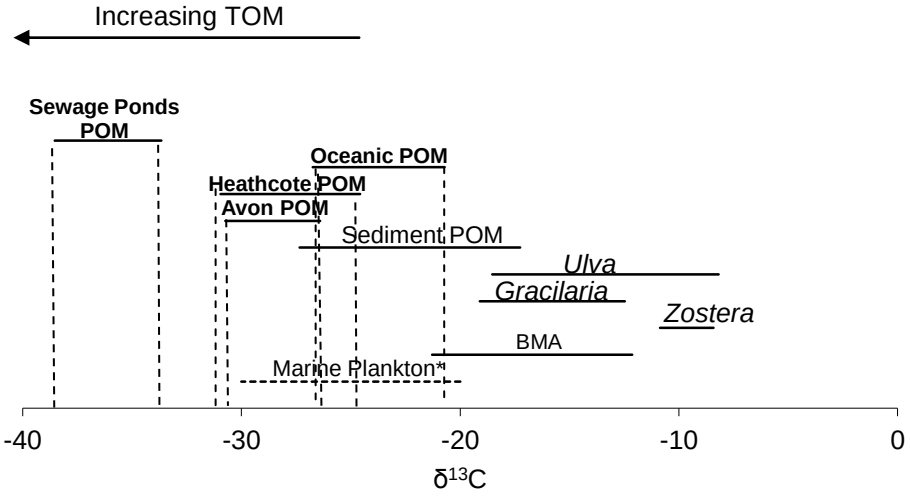

Figure 4.12. Range of $\delta^{13}C$ values of pelagic POM sampled from the sewage ponds, Heathcote river, Avon river and the estuary mouth ("oceanic"). The range in $\delta^{13}C$ values of its potential constituents: BMA, *Gracilaria chilensis*, *Ulva lactuca* and *Zostera muelleri*, are plotted. All values are calculated across all sites and time periods. Dashed lines indicate the regions where potential contributors to pelagic POM from each site are expected to lie. TOM = terrestrially-derived organic matter.

4.3.4. Translocation Experiment

There was no significant change in the $\delta^{13}C$ and $\delta^{15}N$ values of *Amphibola* after transplantation from Discharge to old and new sediments at Heathcote and Humphreys, relative to the isotopic change for this species at Discharge over the translocation period ($\delta^{13}C$: $F_{5,13}$=1.20 p=0.36; $\delta^{15}N$: $F_{5,13}$=0.82 p=0.56). The $\delta^{13}C$ values of *Amphibola* in new sediments at Heathcote and Humphreys were similar but individuals in new sediments at Humphreys had more enriched values of $\delta^{15}N$ (Fig. 4.13A). *Amphibola* in old sediments at Heathcote had slightly enriched isotopic values compared to individuals of this species in new sediments.

Similarly, there were no significant changes in the $\delta^{13}C$ and $\delta^{15}N$ values between transplanted *Austrovenus* and individuals at their source location, Discharge, in October 2011 and January 2012 ($\delta^{13}C$: $F_{5,12}$=2.48 p=0.091; $\delta^{15}N$: $F_{5,12}$=1.64 p=0.22). Individuals of this species transplanted to old sediments at

Humphreys had the highest $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 4.13B). *Austrovenus* sampled from Discharge in January 2012 also showed higher values of $\delta^{13}C$.

Hemigrapsus were taken from Heron and translocated to old and new sediments at Humphreys. Although there were no significant changes in the isotopic values of this species relative to the change at Heron over the translocation period ($\delta^{13}C$: $F_{3,8}=2.16$ $p=0.17$; $\delta^{15}N$: $F_{3,8}=1.64$ $p=0.26$), individuals of this species translocated to new sediments at Humphreys showed more enriched $\delta^{15}N$ and $\delta^{13}C$ values (Fig. 4.13C).

There were significant effects of site, sediment type and their interaction on the $\delta^{15}N$ values of old and new sediments at Humphreys and Heathcote in January 2012 ($F_{1,12}=5.18$; $p=0.04$). In particular, old sediments at Humphreys had $\delta^{15}N$ values that were significantly enriched relative to those of the other sediments sampled. Similarly, there were significant effects of site ($F_{1,12}=212.13$; $p<0.0001$) and sediment type ($F_{1,12}=5.88$; $p=0.032$) on the $\delta^{13}C$ values of sediment, with old and new sediments at Heathcote having more depleted $\delta^{13}C$ values than old and new sediments at Humphreys (Fig. 4.13D).

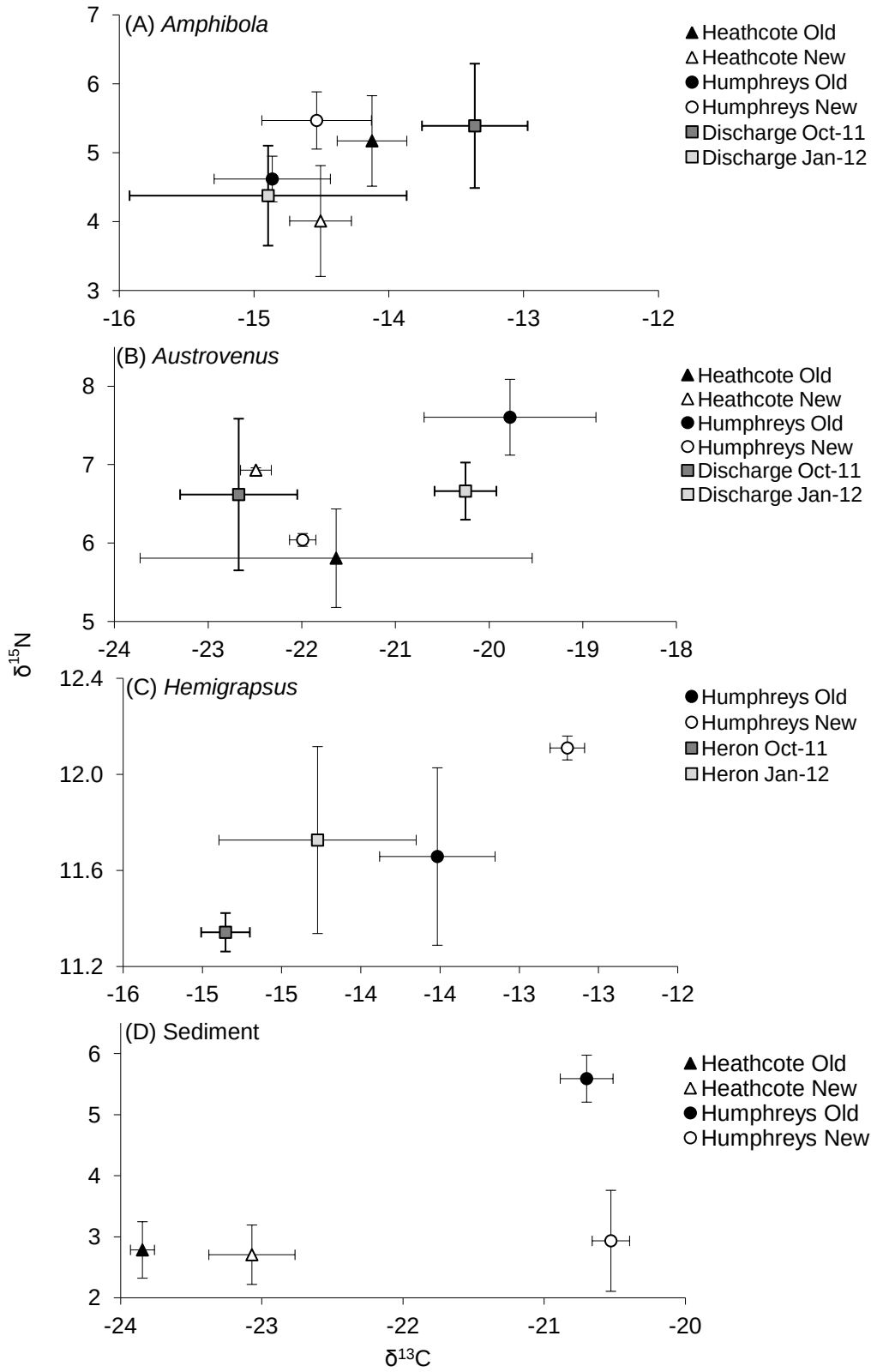

Figure 4.13. Average (±SE) $\delta^{13}C$ and $\delta^{15}N$ values for *Amphibola crenata* (A), *Austrovenus stutchburyi* (B), *Hemigrapsus crenulatus* (C) and surface (<2cm deep) sediment at Heathcote and Humphreys in areas of old and new sediment in January 2012 10 weeks post-translocation. *Amphibola* and *Austrovenus* were sourced from Discharge ($\delta^{13}C$ and $\delta^{15}N$ values of individuals at this site in October 2011 and January 2012 are shown for comparative purposes) and *Hemigrapsus* were sourced from Heron (October 2011 and January 2012 values also shown). N=3.

4.4. Discussion

One of the more surprising conclusions of this study was the relatively large influence of the wastewater diversion and the lesser influence of the earthquakes on the isotopic values of food sources and consumers. Within-taxa, most of the temporal variation in the carbon and nitrogen isotopes related to variations in the uptake of wastewater. This included both wastewater present in the water column and the legacy wastewater stored in the sediments. Consequently, temporal changes occurred mainly at Discharge and were related to the reduced uptake of sewage-derived nutrients after the diversion. The only evidence of any earthquake impacts was seen in the reduced isotopic values of *Ulva*, *Gracilaria* and perhaps *Zostera* after the earthquake due to the uptake of isotopically depleted raw sewage. It was also clear that the massive liquefaction caused by the earthquakes that occurred across the estuary provided relatively pristine sediments that had similar isotopic values across sites. This contrasted the more contaminated and organic-rich old sediments whose spatial variability reflected the characteristics of particular sites.

Most taxa showed considerable site-by-site variation in isotopic values through time. This variation was expected because, unlike in many studies, the sites here were not meant to be replicates of each other. Instead, they were initially chosen to represent the range of conditions found across the estuary (and it should be noted that as the there was a history of study at these sites prior to my study). As indicated, Discharge, situated immediately below the outflow of wastewater from the sewage oxidation ponds, was the most eutrophic site, having accumulated much of the flocculent matter from the outflow over several decades. It was anticipated that taxa and organic matter at this site would reflect those conditions. Indeed, taxa at Discharge had more depleted carbon and nitrogen isotope values, indicating greater assimilation of sewage-derived dissolved inorganic nitrogen (DIN) and dissolved inorganic carbon (DIC) by primary producers and, in turn, consumers. In the middle of the isotopic spectrum were the river sites, Avon and Heathcote. There, consumers had $\delta^{13}C$ and $\delta^{15}N$ values that reflected an uptake of food sources assimilating DIN, DIC and/or POM derived from the rivers that drained large catchments and parts of the city. The ‘oceanic sites’ (Plover and Heron) were influenced by the main tidal flows into and out of the estuary and had higher isotopic signatures reflective of more oceanic conditions.

4.4.1. $\delta^{13}C$ and $\delta^{15}N$ values of food sources

The results showed that different primary producers at the same site did not necessarily have similar isotopic values indicating that they do not necessarily receive nutrients from the same sources (Fig. 4.14). For example, there was considerable variability in the isotopic values of BMA between sites and there were no obvious temporal changes in these values at Discharge after the diversion. This indicates that the nutrient status of BMA is more tightly coupled to processes in the sediments than those in the water column with this producer taking up legacy sediment DIC and DIN. The more depleted values of BMA at Discharge indicates that these nutrients come from sewage-derived sources, as opposed to oceanic/riverine sources at the other sites, where values are more enriched (Rau et al. 1981). These findings are consistent with Hutt (2012) who found that BMA in the Avon-Heathcote Estuary used ammonium stored in the sediments and do not make great use of water column ammonium, a finding also supported by Montgomery et al. (1979), Welsh (1980), Nilsson and Sundback (1991) and Underwood et al. (1998), consequently indicating that changes in the overlying water column do not have a significant effect on the nutrient uptake of BMA. The long term sustained difference in $\delta^{15}N$ values between Heron and Discharge indicates that it is taking considerable time (years) for legacy nitrogen to be removed from sediments. The dramatic reduction in $\delta^{13}C$ values of BMA at Heathcote between August 2011 and August 2012 may be attributable to the fact that a large portion of the Heathcote site was covered in new sediment after the February 2011 earthquake and, consequently, the BMA would have been assimilating DIC with a more enriched isotopic signature after the earthquake (due to no/low amounts of legacy sewage-derived DIC in the new sediments). As the new sediments dispersed and became more incorporated with the surrounding old sediments, the DIC of new sediments would have become more depleted, due to mixing with the higher amount of legacy sewage-derived DIC in the old sediments.

In contrast to BMA, the similarity in the isotopic values for (each of) *Ulva* and *Gracilaria* at Heron (less eutrophic) and Humphreys (highly eutrophic) indicates that these species are taking up the bulk of their nutrients directly from the water column rather than from the sediments (Fig. 4.14). Further evidence for this is provided by the dramatic change in the isotopic values of these species after the earthquake, due to the input of raw sewage into the water column. These species appear to be

reflecting the conditions present in the water column and this supports literature that report some algae (particularly *Ulva* spp.) to be quick responders to changes in nitrogen concentration due to high biomass turnover rates (Lapointe and Tenore 1981, Rosenberg and Ramus 1982, Bjornsater and Wheeler 1990, Tarutani et al. 2004, Cornelisen et al. 2007). Although *Gracilaria* has a slower growth rate and tissue turnover time (i.e., it is likely to be integrating stable isotopes over a longer period (Rosenberg and Ramus 1982)) the isotopic values of this species still showed a clear reduction after the earthquake.

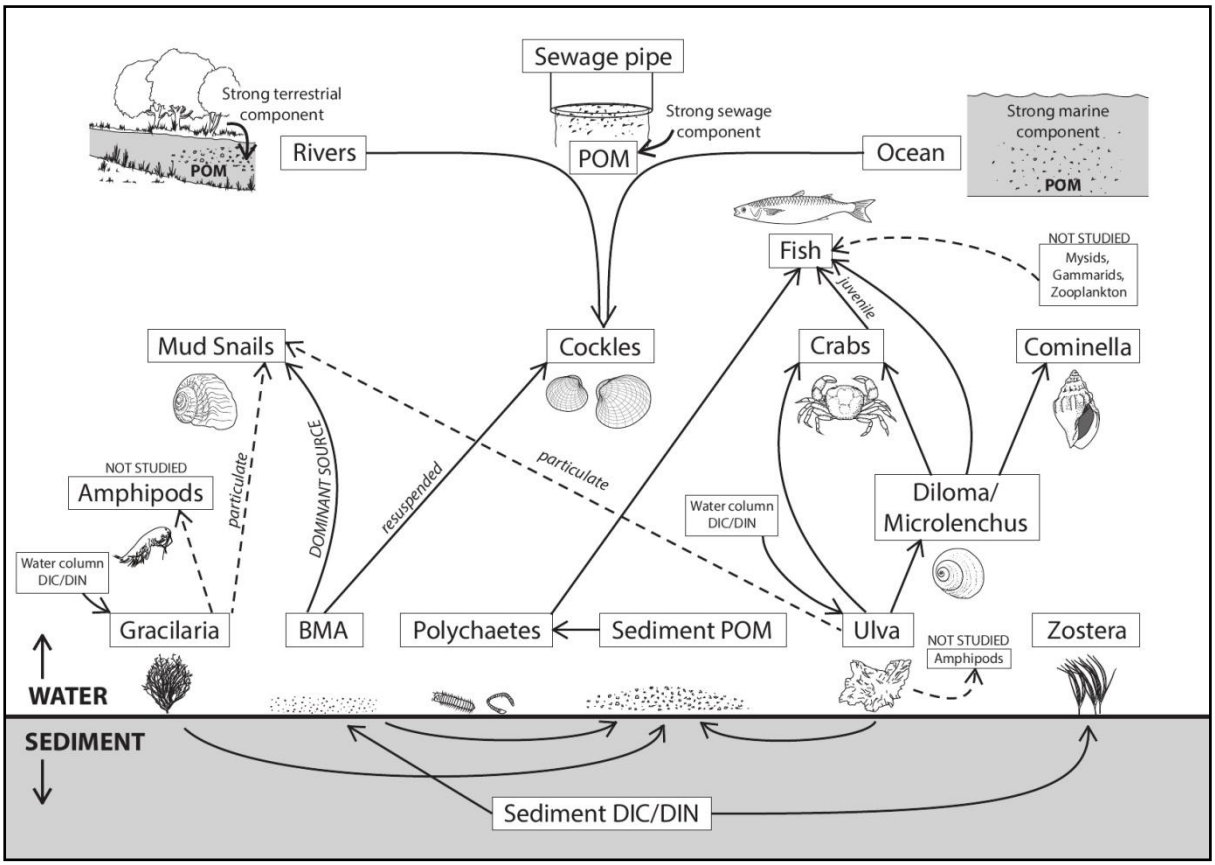

Figure 4.14. Synthesis of the food web dynamics occurring in the Avon-Heathcote Estuary

The enriched isotope values for *Ulva* during the initial sampling periods may be explained by the influences of gradients in irradiance, salinity and water motion (Cornelisen et al. 2007). For example, carbon signatures of macroalgae can become more enriched under levels of high irradiance due to a greater carbon demand leading to the assimilation of the more isotopically-enriched HCO_3^-, rather than CO_2 (aq), that is more depleted (Wefer and Killingley 1986, Kubler and Raven 1995). As such, the enriched $\delta^{13}C$ values seen in the initial sampling periods, that were also in

summer, may reflect the increased irradiance occurring during this time period. Water motion can influence carbon and nitrogen isotopes, with the hydrodynamic regime influencing the proportion of HCO_3^- versus CO_2 being taken up by algae. But, it is most likely that the data for the initial sampling periods for *Ulva* does not represent the true picture. In-depth sampling done by Barr (2012) across five sites and six time periods between November 2009 and March 2010, prior to the diversion, showed a high level of variability in the $\delta^{15}N$ values of *Ulva* (from ~2‰ to 16‰) during this period, the average of which is not greatly different to values seen after the diversion.

Although it could not be concluded from the data (due to the reduced temporal and spatial occurrence of *Zostera*), it is most likely that *Zostera* is receiving much of its nutrition from sediment sources, via its roots (Fig. 4.14). The $\delta^{15}N$ values of this species were similar to those measured for *Zostera* sp. by Machas et al. (2003) in Ria Formosa, Portugal, by Bode et al. (2006) in estuaries of the NW Iberian peninsula (5.6‰) and by Jephson et al. (2008a) along the Swedish coast (~5‰). The $\delta^{13}C$ values were also within the range of those reported by other studies (Jephson et al. 2008b, Baeta et al. 2009b). The high variability of *Zostera* stable isotope values in my study may reflect a seasonal trend, with most enriched values occurring in summer, due to an increased uptake of the more enriched HCO_3^- under high irradiance conditions (as seen for *Ulva*). A longer temporal dataset is, however, required to confirm this.

Sediment POM is complex as it consists of various (potential) components: BMA, macroalgal/marine plant detritus and other forms of organic matter, from ocean, riverine, terrestrial and sewage-derived origins (Peters et al. 1978, Wada et al. 1987). The most depleted $\delta^{13}C$ values found for sediment from the Discharge site indicate a greater incorporation of isotopically-deplete organic material, likely of sewage-derived origin. The increase in $\delta^{13}C$ values at this site over time indicates a reduction in the proportion of sewage-derived material contributing to the POM. More enriched values of $\delta^{13}C$ at Heron and Pukeko indicate a greater proportion of oceanic-derived POM, whereas slightly lower values at the riverine sites indicate a greater proportion of riverine/terrestrial-derived organic matter contributing to the total POM pool. Higher temporal variability in $\delta^{13}C$ signatures of sediment POM at Heron and Pukeko may be explained by temporal variability in macroalgal biomass (and subsequently, macroalgal detrital biomass in the sediment). Similarly, high

variability in $\delta^{15}N$ values seen across the sites may reflect the change in relative contributions of different POM components at different sampling periods.

The higher $\delta^{13}C$ values of old sediments, and their increased range of $\delta^{13}C$ values, indicates a contribution of marine-derived organic matter (BMA and macroalgae) to their composition. The $\delta^{13}C$ values of new sediments are, however, outside the range of values for any of the marine-derived organic matter examined. This indicates that any organic matter in these sediments is derived from terrestrial sources and, due to the particularly low values, may be archaic in origin. The isotope values indicate that inadequate time had passed for this new sediment to accumulate any significant quantities of marine-derived organic matter and/or any physical mixing with the surrounding old sediments to occur.

Due to the high quantities of detrital material in the Avon-Heathcote Estuary, and the difficulties in separating phytoplankton from other pelagic POM, I was not able to provide separate isotopic values for phytoplankton and other forms of pelagic POM. Consequently, the pelagic POM sampled was (potentially) comprised of different mixes of detritus (marine, terrestrial and/or sewage-derived) and plankton (riverine, estuarine and/or oceanic) (Hopkinson et al. 1998, Sakamaki and Richardson 2008). The ranges of $\delta^{13}C$ values found for pelagic POM agrees with those reported in the literature, with riverine POM < marine POM (< BMA), indicating a greater influence of marine-derived POM at the estuary mouth than at the rivers (Sakamaki and Richardson 2009). Particulate organic matter collected from the treatment ponds was the only pelagic POM to show a clear signal, with relatively depleted $\delta^{15}N$ values, but also high variability. Chaves (2004) also reported sewage POM to have depleted isotopic values.

4.4.2. $\delta^{13}C$ and $\delta^{15}N$ values of consumers and trophic relationships

In general, $\delta^{13}C$ and $\delta^{15}N$ values of consumers, particularly *Austrovenus* and *Amphibola*, showed a strong localised point-source eutrophication effect. The enrichment of the isotope values of *Austrovenus* at Discharge throughout the sampling period indicates a reduction in the uptake of food sources using sewage-derived DIC/DIN and/or POM/POC. The more enriched isotope values at the oceanic sites relative to the riverine sites reflects an increased uptake of food sources assimilating marine- versus riverine-derived DIN and DIC sources. Assuming a trophic enrichment of $\delta^{13}C$ and $\delta^{15}N$ at 1‰ and 3‰ respectively, the estimated $\delta^{13}C$

values of *Austrovenus* diet, over all spatial and temporal scales, falls within the range of values for BMA, ocean POM, *Ulva* and *Gracilaria*. The $\delta^{15}N$ values of these food sources also fall within the range of those for *Austrovenus*, except POM, that is more depleted. It is, however, unlikely that this indicates that POM is not contributing to the diet of *Austrovenus,* rather it suggests the amount of trophic fractionation occurring between POM and its consumers is much higher than 3‰ (Post 2002). Based on the dual $\delta^{13}C$ versus $\delta^{15}N$ biplots, and what is known about this species, it is most likely that *Austrovenus* is consuming a combination of POM (mostly oceanic) and re-suspended BMA. Overall, the results support literature describing the filter-feeding ecology of *Austrovenus* and work by Leduc et al. (2006) who report seston to contribute up to 77% of *Austrovenus* diet. But, the finding of substantial uptake of BMA by *Austrovenus* was interesting and indicates there to be significant amounts of BMA resuspension occurring in water column of the Avon-Heathcote Estuary. From other aspects of my work (*Chapters 2, 3* and *5*) and work done by Hutt (2012) we know there are areas in the estuary with a high biomass of BMA. Consequently, the significant contribution of BMA, alongside POM (Fig. 4.14), to *Austrovenus* diet suggests an adaption to the food sources available in this estuary. Other studies have reported tight nutritional linkages between BMA and suspension feeding bivalves, reporting that resuspended BMA can contribute an important component to the diets of these clams (Shumway 1987, Sauriau and Kang 2000, Hailes 2006).

Similar to *Austrovenus*, *Amphibola* also showed lowest isotope values at Discharge but the $\delta^{15}N$ values of *Amphibola* did not show an overall enrichment over time. This is probably due to the uptake of sediment nitrogen by BMA that maintains the $\delta^{15}N$ values of the microalgae at a relatively depleted level throughout the study period (and *Amphiobla* are consuming the BMA). *Amphibola* also showed no clear separation of $\delta^{15}N$ values between the riverine and oceanic sites. Again, this probably relates to the DIN sediment sources being taken up by the BMA and suggests that the composition of sediment DIN is not different between the oceanic and riverine sites. Benthic microalgae were found to be a key food source contributing to the diet of *Amphibola* (Fig. 4.14), supporting literature that reports *Amphibola* to graze on BMA (Juniper 1982, 1987, Hutt 2012). Leduc et al. (2006) also found BMA to contribute to >90% of *Amphibola* diets, when using $\delta^{13}C$ and $\delta^{15}N$ stable isotopes. Although there was considerable overlap of the isotopic signatures of *Gracilaria/Ulva*, and *Amphibola*, it is unlikely that these algae are contributing a

significant proportion to the diet of *Amphibola*, and that any uptake of these food sources by the snail will be in their particulate form. The sampling of BMA was restricted to locations where there were obvious BMA mats. The frequency of BMA sampling was also less than that of the sampling of its consumers. These are the likely reasons explaining the non-overlapping range of $\delta^{13}C$ values of BMA and *Amphiobla* at the oceanic sites, and it is likely that this is still the dominant food source of this species at these sites. Thus, spatial and temporal changes in the isotopic composition of *Amphibola* probably reflected changes in the isotopic composition of its food sources, not a switch in diet.

In general, the isotopic values of crabs were more variable and more depleted at the eutrophic site, reflecting variability in the isotopic values of their food sources which was higher at Discharge. The isotopic signatures of crabs were more depleted at this site due to a greater proportion of sewage-derived DIC/DIN being taken up by their food sources. Reductions in the $\delta^{13}C$ and $\delta^{15}N$ values of *Microlenchus* and *Diloma* between January 2011 and January 2012 may reflect reductions in the isotopic composition of their food sources, predominately *Ulva*, that showed lower isotope values during this period due to the influx of raw sewage from the earthquakes. *Cominella* are carnivorous feeders and as such, the absence of any change in their isotopic signatures over the 12 month period is not surprising, considering no/little change was seen for other invertebrates at the site where they were collected. The spatial and temporal variability seen in the isotopic values of polychaetes reflects the variability in the isotopic signatures of organic matter being consumed by these invertebrates. *Diloma* and *Microlenchus* were found to have diets dominated by *Ulva* that supports observations in the field where these species are often found attached to *Ulva* fronds that appear to be eaten. The findings do not, however, agree with Leduc et al. (2006) who found BMA to contribute >90% to the diet of *Diloma*. This discrepancy may be due to sampling by Leduc et al. (2006) being in a relatively low nutrient environment, with presumably a low biomass of *Ulva*, compared to the high biomass of *Ulva* occurring in the Avon-Heathcote Estuary that *Diloma* may be feeding opportunistically on. From the trophic position of the fish species, they are likely feeding on juvenile crabs and polychaetes, as well as other small crustaceans, such as mysids, gammarids and zooplankton that were not studied. This agrees with literature that reports many motile decapods to share detrital food sources with infaunal and epifaunal species, or to prey directly on these

primary consumers (Bemvenuti 1987, Kapusta 1998). With the possible exception of *Amphibola* at the oceanic sites, there was no evidence that any of the consumers studied were directly consuming *Zostera*. This supports the notion by other authors that many consumers can only use seagrass once it becomes microbially altered and available as detritus (Tenore et al. 1982, Vizzini and Mazzola 2002).

The results from the transplantation experiment showed no effects of transplantation on the isotopic values of consumers. Although there were some emerging trends of change in $\delta^{15}N$ and $\delta^{13}C$ values of transplanted individuals relative to their source population, almost all changes were within the range of change seen for each species over the same time period at their source location. It is likely that the relatively small (N=3) number of individuals sampled from each treatment, and the relatively short experimental duration (10 weeks) may have affected the experimental results. Although a larger number of individuals of each species were translocated to old and new sediments at Heathcote and Humphreys, the majority of them did not survive beyond two months, and hence the timeframe of the experiment was adjusted from that which was initially planned (4-6 months). This caused issues not only with regards to the final number of individuals that were available for stable isotope analysis, but also with regards to a reduced period of time available for the turnover of the muscle tissue sampled. Muscle tissue has a slow turnover rate relative to other tissues, such as liver, heart, gill, blood, eye and gonad (Shurin et al. 2006, Singer and Battin 2007, Tewfik et al. 2007) and although there are no known studies examining the muscle tissue turnover rates of the species sampled in the present study, experimental studies on sand goby state half-lives of $\delta^{15}N$ and $\delta^{13}C$ to be 28 and 25 days respectively (Tewfik et al. 2007), blue crabs to be 39 and 22 days respectively (Tewfik et al. 2007) and summer flounder to be 49 to 107 days for both isotopes (Shurin et al. 2006). Thus, it is possible that the translocation period in this study was not sufficient to observe changes in the isotopic values of the consumers. Consequently, repeating this experiment, using a larger number of transplanted individuals, and transplanting over a longer time frame (or sampling tissues with a faster turnover rate) would likely produce more robust results.

To be able to use stable isotopes to infer information about an animal's diet, distinct differences in the isotopic values of all potential food sources is required. Due to the large number of food sources and consumers examined in this study, as

well as the significant eutrophication and salinity gradients from which they were sampled, isotopic values of food web components were not always distinct and often showed large variability. Consequently, I was not able to apply mixing models and clearly conclude the exact food sources and quantities contributing to consumer diets. But, to the best of my knowledge, there are no other studies that have examined the isotopic composition of such a large number of food web components over such a long temporal period, and wide spatial scales. Despite the challenges this has caused when attempting mixing models, it has undoubtedly provided a more comprehensive, detailed and true picture of an estuarine food web than studies that examine trophic relationships of a reduced number of food web components on a single sampling occasion.

4.4.3. Wider implications

Estuarine ecosystems are characterised by inputs of organic matter from terrestrial and marine sources, and these, alongside primary producers, macroalgae, microalgae and seagrasses, form the base of estuarine food webs (Ishihi 2003). The results of this study agree with other stable isotope studies that suggest that riverine terrestrial organic matter, in comparison to autochthonous organic matter, is relatively unimportant in supporting estuarine food webs (Simenstad and Wissmar 1985, Peterson and Howarth 1987, Sullivan and Moncreiff 1990, Deegan and Garritt 1997, Kurata et al. 2001, Takai et al. 2002). The results are also consistent with a growing number of studies that report BMA to be the overall most important food source supporting macrobenthic communities, with variations in its importance based on site and species type (Lee 2000, Ishihi 2003, Kang et al. 2003). Nutrient uptake by BMA is tightly coupled to the nitrogen dynamics at the sediment-water interface, which in turn is affected by both current and historical nitrogen inputs to the area. Interestingly, in areas of high nutrient input, BMA biomass tends to be high, that suggests that a higher biomass of secondary production can be supported. But, this does not consider 1) the reduction in nutritional/health quality of BMA taking up sewage-derived DIN/DIC, 2) that in highly eutrophic areas where BMA flourish, many invertebrates will not be able to tolerate the high nutrient conditions, hence consumer biodiversity will decrease, and 3) BMA occurs little or no habitat protection due to it being flush with the sediment surface and offering no 3-dimensional structures for shelter and hiding. Consequently, an “optimal” estuarine food web, supported

predominately by BMA, is unlikely to occur under eutrophic conditions. The results also support the vital functional role that macroinvertebrates play as the intermediate trophic link between primary producers (and POM) and top predators, like crabs, fish and seabirds, in estuarine food webs (Lopez and Levinton 1987, Herman et al. 1999, Middelburg et al. 2000, Canuel et al. 2007). In areas becoming more or less eutrophic, successional changes in community composition will occur, altering competition for food sources and predator-prey interactions, and changing the structure of communities through top-down (consumption) and bottom-up (resource availability) pathways (Armitage and Fourqurean 2009). These have the ability to change the structure of estuarine food webs, or change the end-member nutrient sources that are taken up by primary producers and consequently support secondary production, the latter of which was seen at Discharge in this study.

4.4.4. Summary

The Avon-Heathcote Estuary, like most estuaries, is an estuary of complex co-occurring gradients. This has been reflected in the isotopic results with food sources and consumers showing a general trend of more depleted $\delta^{13}C$ and $\delta^{15}N$ values in more anthropogenically affected areas and more enriched values nearer the estuary mouth. Temporal variation in $\delta^{13}C$ and $\delta^{15}N$ values was most evident at the most eutrophic site, Discharge, and least evident at the most oceanic site, Pukeko. Discharge was the only site showing a definite trend, with $\delta^{13}C$ and $\delta^{15}N$ values increasing over time. This appears to be a delayed response to the diversion as opposed to a response to earthquake events. These results supported my hypothesis that food sources and consumers from more eutrophic sites would have isotopic signatures that were more depleted than food sources and consumers at the other sites, and that these differences would decrease after the diversion due to the cessation of sewage inputs to the estuary. Inconsistent with my hypothesis however, I found that primary producers at the same site were not necessarily receiving nitrogen from the same source, with BMA using mainly nutrients from the sediment, and *Ulva* and *Gracilaria* taking up water column DIN/DIC. The results also showed that although primary producer assemblages in the estuary have changed in response to eutrophication and disturbance events (*Chapters 2* and *3*), the primary producers supporting estuarine consumers seem to be independent of their relative biomass. i.e., the diet of specific consumer species across spatial and temporal

scales was similar (despite spatial and temporal differences in the biomass of primary producers) and variations in isotopic values were due to changes in DIN/DIC source, not changes in diet. Benthic microalgae were found to be an important food source for both *Amphibola* and *Austrovenus*, supporting my hypothesis for *Amphibola* but not *Austrovenus.*

Overall, the results of this study have refined our understanding of trophic relationships and overall food web structure in environments affected by eutrophication. I have demonstrated stable isotope analysis to be an effective tool in determining eutrophication conditions in primary producers, other basal food sources and estuarine consumers. With an increasing number of estuaries worldwide becoming more eutrophic, long-term monitoring of natural stable isotope values across a range of spatial and temporal scales is important in increasing our understanding of the impacts of eutrophication on food web dynamics in these areas.

Chapter Five

Estuarine Ecosystem Functioning after Disturbance: Role of Sediments and Invertebrates on Primary Production and Biogeochemical Flux

5.1. Introduction

Disturbances and eutrophication can affect both the structure of aquatic ecosystems and their functioning (Snelgrove et al. 1997, Lee et al. 2011). Ecosystem functioning (i.e., the processes occurring within a system) can be affected by biotic and abiotic components, which can include changes in sediment composition, biogeochemical gradients (sediment oxygen and nutrient profiles), the availability of food resources, and faunal and marine plant biodiversity (e.g., species loss, and behavioural and compositional changes) (Thistle 1981, Widdicombe and Austen 2001). There are many processes that contribute to, and can be used to define, the functioning of ecosystems. These include primary production, the flux, uptake and recycling of nutrients, bioturbation, biomass accumulation, mineralisation, the burial of sediment to remove organic and inorganic compounds, and decomposition rates (Schwartz et al. 2000, Aller 2001, Giller et al. 2004, Norling et al. 2007). Of these, primary production is probably the most widely measured because rates of oxygen flux across the sediment-water interface can provide a quantitative measure of ecosystem functioning by showing levels of respiration and primary production and indicating whether an area is in net autotrophy or heterotrophy (Schwartz et al. 2000). Furthermore, by examining the flux and uptake of nutrients, such as ammonium (NH_4-N), nitrate-nitrite (NO_x-N) and/or phosphate (PO_4^{3-}), the role of bottom-up drivers can be identified. This can provide insight into the possible mechanisms underpinning primary production in a particular system (Lohrer et al. 2010).

In eutrophic areas, quantifying the efflux of nutrients (particularly nitrogen and phosphorus) from sediments provides useful insight into differences among sites (or along a eutrophication/disturbance gradient), or the degree of success of remediative measures. For example, efflux studies can show whether remediative interventions have been successful in accelerating ecosystem recovery by either removing (dredging) or burying (capping) nutrient-rich substrate. Capping involves sealing the sediment off from the water column by placing a cover over the sediment to minimize the release of nutrients (or other pollutants). Experiments have been carried out, mostly in lakes, using sand, gravel, or non-natural materials (e.g., zeolite, ceramicite and light porous media which react with and remove ammonium), to cap sediments (Wang et al. 1991, Zeman 1994, Huang et al. 2011). In some cases, 90-100% of total nitrogen in the overlying water has been removed by capping sediments (Huang

et al. 2011). It must be remembered, however, that nitrogen flux is also going to depend on microbial nitrogen regeneration (from organic matter remineralisation), macrofaunal nitrogen excretion, microbial nitrogen uptake (ammonium taken up by nitrifiers, nitrate+nitrite taken up by denitrifiers) as well as any photosynthetic uptake by marine plants.

Many studies have examined the functioning of soft-sediment ecosystems and the role of fauna in this process (e.g., Botto and Iribarne 2000, Lohrer et al. 2004, Webb and Eyre 2004, Gibbs et al. 2005, Lohrer et al. 2005, Giles and Pilditch 2006, Hewitt et al. 2006, Thrush et al. 2006, Norling et al. 2007, Sandwell et al. 2009, Lohrer et al. 2010, Wang et al. 2010, Jones et al. 2011, Needham et al. 2011). Most studies examining biodiversity and ecosystem functioning use manipulative field experiments (Bulling et al. 2006), which usually indicate there is a positive relationship between an increase in biodiversity and an increase in ecosystem functioning (Lohrer et al. 2010). Consistent with this relationship, a reduction in biodiversity resulting from a disturbance will therefore result in a reduction in the functioning of the ecosystem. It follows that subsequent increases in biodiversity, as the ecosystem recovers, will then increase functioning (Elliott et al. 2007, Rossi et al. 2009, Van Colen 2009, Lohrer et al. 2010). However, different organisms will recover at different rates, altering the recovery trajectory of the whole disturbed environment. For example, benthic microalgae (BMA), microscopic primary producers inhabiting the sediment surface, and some algal species, generally recover faster than seagrasses and macrofauna (Larson and Sundback 2008, Montserrat et al. 2008, Lohrer et al. 2010). In shallow estuaries, BMA are not only an important food source for heterotrophic consumers (see *Chapter 4* and Underwood and Kromkamp 1999, Cook et al. 2009) but they also play an important role in modulating the rate and direction of nutrient flux (via photosynthetic nutrient uptake) and influencing primary production (Sundback et al. 2000). Relationships between BMA and the flux of oxygen and nutrients are, however, controlled by BMA abundance among other factors. In turn, this is influenced by grazing and other activities of estuarine fauna (Thrush et al. 2006).

Bioturbation, the biological reworking of sediments causing alterations in the local structures or topographic features (Biles et al. 2002, Meysman et al. 2006), is an important process done by benthic fauna in estuarine environments (e.g., Lohrer et al. 2004, Hewitt et al. 2006, Thrush et al. 2006, Sandwell et al. 2009, Jones et al.

2011, Needham et al. 2011). This process can modify hydrodynamic, biogeochemical and particle gradients in the sediment, oxic/anoxic boundaries, the permeability and water content of sediments, and the subduction of organic matter, all of which impact rates of oxygen, nutrient, reactant and metabolite flux across the sediment-water interface and remineralisation (Aller 2001, Lohrer et al. 2004). Large organisms are particularly important bioturbators but their relative impact on oxygen and nutrient flux is highly dependent on their activity patterns and individual species traits. This can be attributable to differences in 1) sediment mixing (bioturbation) and irrigation (bioirrigation) activity, 2) feeding guilds (e.g., grazer versus suspension versus deposit feeder), 3) the impacts of species on algal diversity and abundance (links to primary production), and 4) the production of biodeposits (faeces and pseudo-faeces) among species (Loreau et al. 2001, Bolam et al. 2002, Giller et al. 2004, Hooper et al. 2005). Thus, it has been reported that functional diversity (i.e., functional group richness, species identity and the influence of one or a few “key” species) is more important than species richness in influencing ecosystem functioning (Emmerson et al. 2001, Waldbusser et al. 2004, Raffaelli 2006, Norling et al. 2007). For example, fauna that build networks of burrows and bioturbate deep sediments, such as some crab and polychaete species, will generally release nitrogen from the sediment by increasing the surface area available for nutrient exchange through their activities that increase the mixing, penetratability and erodibility of sediments (Botto and Iribarne 2000, Escapa et al. 2008, Needham et al. 2010, Wang et al. 2010, Needham et al. 2011). In contrast, taxa that live on or near the surface, like many gastropods, destabilise only surface sediments and are perhaps less likely to release nutrients from the sediments, although faeces produced at the sediment surface may increase nitrogen concentrations. Grazers will negatively impact BMA abundance, affecting the photosynthetic uptake of nutrients and oxygen, and consequently impacting primary production. Filter-feeders, such as bivalves living in the top layers of the sediments, generally bioturbate only surface sediments. These organisms produce biodeposits and consequently oxygen and nutrient flux in areas containing these taxa are often tightly coupled with this (Gibbs et al. 2005, Giles and Pilditch 2006, Thrush et al. 2006, Sandwell et al. 2009, Jones et al. 2011). There is also growing evidence that the functioning of species can be habitat-dependent, with several studies showing that habitat characteristics such as sediment type can alter the impact of particular species on primary production and

nutrient flux (Lohrer et al. 2010, Jones et al. 2011, Needham et al. 2011). Thus, the process of nutrient and oxygen flux is complex and influenced by important direct and indirect interactions among the system components. It depends not only on the biotic components, but also on physical features of the habitat and the chemical gradients that exist within it.

Few experimental studies have examined the effects of disturbance or stress on ecosystem functioning in aquatic environments. Most of these do so indirectly by manipulating species richness, diversity, or sediment characteristics, or by carrying out experiments along natural gradients of nutrients and/or sedimentation and making comparisons between impacted/manipulated and non-impacted/non-manipulated sites (Gibbs et al. 2005, Lohrer et al. 2010, Rodil et al. 2011, Lohrer et al. 2012, Villnas et al. 2012). The 2011 earthquakes in Christchurch provided a unique opportunity to examine the impacts of a large-scale natural physical disturbance on the functioning and recovery of the Avon-Heathcote Estuary. After these earthquakes, large areas of the estuary were covered in liquefaction ("new sediments") which were coarser and had lower levels of organic content and pollutants than the surrounding "old" sediments. Full details of the impacts of the earthquake on the physical and biological features of the estuary are given in *Chapter 3*. Given the significant impact of the earthquakes on sediments and communities within the estuary, I was interested in how these disturbances had affected its functioning. My aims were to examine 1) whether the capping of eutrophic sediments (via natural processes) had reduced the efflux of legacy nutrients (and thereby accelerated estuarine recovery), and 2) how primary production (used as a proxy for ecosystem functioning) varied between old and new sediments. To do this, I incubated areas of old and new sediments, using dark and light benthic chambers, to examine *in situ* levels of oxygen and nutrient flux. This was done at various sites 2 months, 7 months and 10 months after the February 2011 earthquake. In addition to this, I was interested in how changes in invertebrate communities, brought about by disturbances such as this, can affect ecosystem functioning. To investigate the influence of invertebrate functional guild on ecosystem functioning, a laboratory experiment was done comparing the effects of *Amphibola crenata* (surface grazer), *Austrovenus stutchburyi* (filter-feeder), and *Austrohelice crassa* (burrow-builder) on primary production and nutrient cycling in old and new sediments. I investigated the mechanisms responsible for differences by

exploring relationships between primary production, nutrient (NH_4-N, NO_x-N, PO_4^{3-}) flux, Chl *a* concentration (BMA biomass) and sediment composition.

I hypothesised that:

- nutrient (especially NH_4-N) efflux would be greater in old sediments than in new sediments after the earthquake. The capping of eutrophic old sediments with clean new sediments was expected to reduce nutrient release. As old and new sediments mixed over time, I expected levels of nutrient efflux to become more similar between the two sediment types.
- gross primary production (GPP) would be greatest in old sediments because these sediments appeared, visually, to have a higher biomass of BMA. This assumed a positive correlation between GPP and BMA biomass. However, I also expected this to be driven by greater nutrient (especially NH_4-N) release in old sediments (nutrients are a requirement of photosynthesis and NH_4-N is the most readily utilisable form of nitrogen).
- the addition of *Amphibola*, a surface grazer, would reduce BMA biomass and consequently levels of GPP in old and new sediments. Nutrient flux in this treatment was expected to be slightly increased relative to the control due to the production of faeces at the sediment surface and the enhanced release of nutrients from surface sediments.
- as *Austrovenus* occurs mainly beneath the sediment surface and can bulldoze surface sediments, I expected NH_4-N efflux in this treatment to be higher than in the control treatment. I expected GPP to be similar or slightly elevated relative to the control.
- *Austrohelice* treatments would show reduced levels of GPP. This would be attributable both to the consumption of BMA and its burial from bioturbation. However, as this species has shown different burrowing behaviours in different sediment types (Needham et al. 2011), I expected less bioturbation in the cohesive old sediments (once the burrows were constructed they were not expected to advect much sediment). In the sandier new sediments, burrows were expected to collapse more frequently and hence greater sediment advection (bioturbation) was expected.

5.2. Methods

5.2.1. In situ sampling

5.2.1.1. Sites

Sampling was done at four sites (Discharge, Heathcote, Heron and Humphreys) in Christchurch's Avon-Heathcote Estuary. A description of each site and a map showing their location is given in *Chapter 1: General Introduction*. Briefly, Discharge is a eutrophic site situated below the former discharge pipe of the Bromley Oxidation Ponds. Prior to March 2010, this pipe discharged approximately 500,000m^3 of wastewater into the estuary daily (URS 2004). This was also one of the main sites for sewage entering the estuary after the earthquake on 22 February 2011. Humphreys is situated in a low-flow "back-water" area about 0.5km from Discharge where it also received high amounts of sewage-derived nitrogen. Because of low tidal flows and circulation at this site, the sediments had accumulated high amounts of organic matter and legacy nitrogen. Heathcote is an estuarine site near the Heathcote River mouth and consequently exposed to greater amounts of riverine and terrestrial inputs. Large amounts of wastewater and sewage entered the estuary via this river after the earthquakes. Heron is situated nearest the estuary mouth on the eastern side of the estuary and is the least eutrophic site.

These sites were chosen because new sediments were produced in these areas by the February 2011 earthquake. Old and new sediments differed in their composition and biological and chemical properties. New sediments were coarser, had less organic matter and fewer pollutants (detailed in *Chapter 3*).

5.2.1.2. Incubation and sampling protocol

Fluxes of oxygen and nutrients (NH_4-N, NO_x-N, PO_4^{3-}) across the sediment-water interface were measured *in situ* using custom-designed and built benthic chambers. Chambers were made of clear plastic and were cylindrical with one closed end (above the sediment) and one open end (inserted into the sediment) and had a height of 16cm (Fig. 5.1). They covered an area of 0.0153m^2 of the sediment surface and when inserted into the sediment to the pre-determined depth, trapped 1L of seawater. Two lengths of rubber tubing (5mm internal diameter) extended from the top of the chamber. At 90cm in length, the longer tube was used to extract water samples from the chamber via a one-way leur lock valve enabling the attachment of

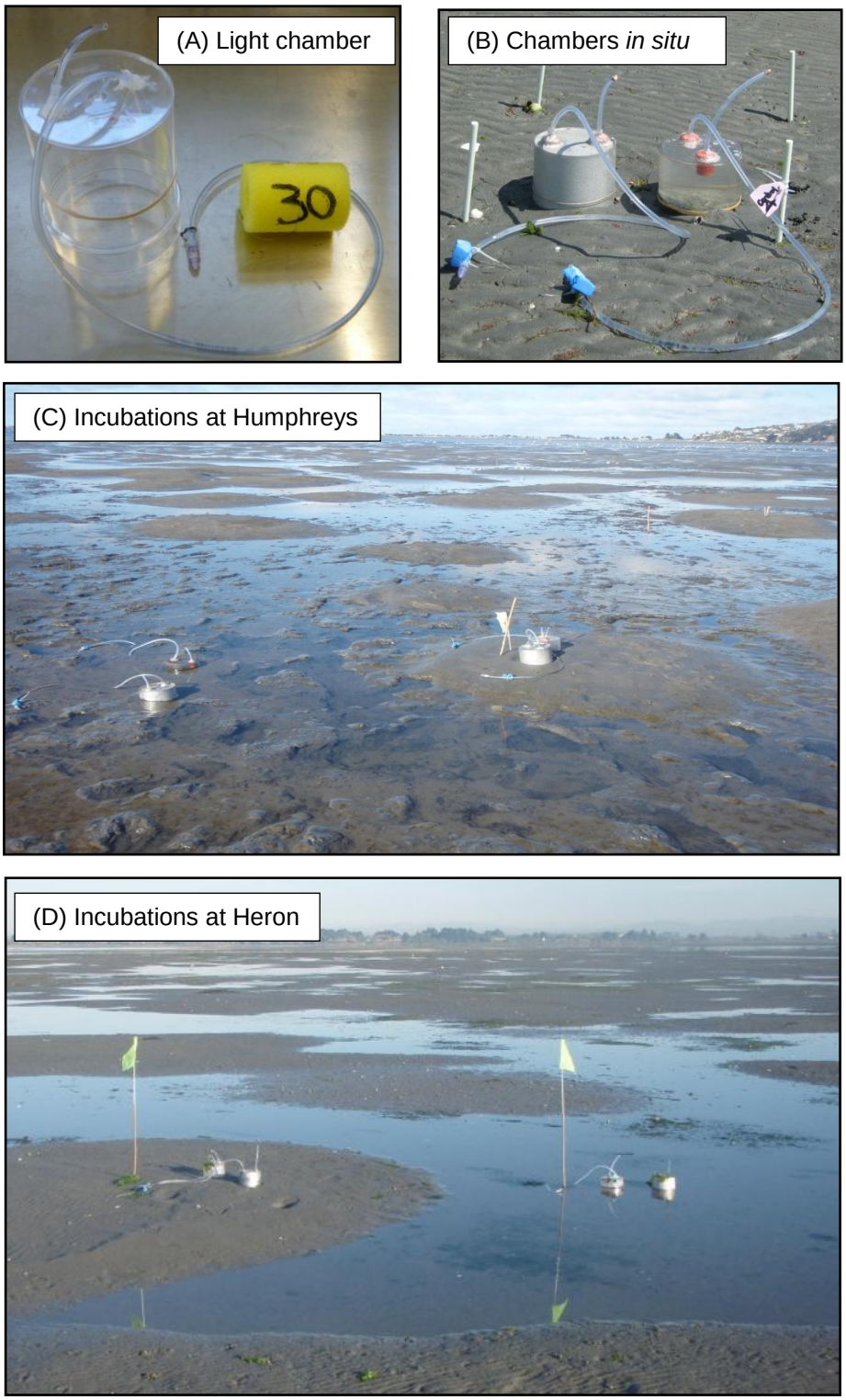

Figure 5.1. Photographs of benthic chambers and incubations. A: light benthic chamber, B: dark (left) and light (right) benthic chambers *in situ*, C: incubations at Humphreys in old (left) and new (right) sediments, D: incubations at Heron in old (right) and new (left) sediments. Note that incubations occurred at high tide.

a 60mL syringe. The shorter tube, 10cm in length, acted as a channel for compensation water to enter the chamber after sample extraction, allowing for the displacement of water during the sampling procedure. This setup ensured no air bubbles entered the chamber at any stage throughout the incubation. To measure total oxygen utilization (TOU) and nutrient availability, incubations under dark conditions were also required. Thus, dark chambers were also built which were identical to the light chambers but were painted silver (Fig. 5.1).

Incubations were done at Discharge, Humphreys and Heron at high tide on a sunny day in April 2011. Four areas of old sediment and four areas of new sediment were selected at each site. Once the depth of the water at the incubation site reached approximately 20cm (i.e., the depth of water exceeded that of the inserted chambers), one dark chamber and one light chamber were inserted into each area of old and new sediment (N=4). Equal pressure was applied to each side of the chamber while pushing it gently into the sediment. Care was taken to ensure minimal disturbance to the surrounding sediment and that the chamber was filled with water and contained no air bubbles. Chambers were then left for at least 30 minutes to allow any sediment disturbed during the insertion process to settle before sampling began. After this, a clean 60mL syringe was attached to the one-way leur lock on the sampling tube and an initial 20mL sample extracted, and discarded, to clear the sampling tube. Two subsequent 60mL samples were then extracted. The first sample was immediately analysed in the field for dissolved oxygen content using a HACH HQ 30d probe. The second sample was collected for nutrient analysis. It was filtered through a Whatman GF/C filter (retention 1.2µm), into an acid washed bottle, placed on ice in the dark and transferred to a -20°C freezer as soon as possible. After the completion of the first round of sampling, chambers were left for approximately 2h before being re-sampled in an identical way (to determine changes in oxygen and nutrient concentrations over the incubation period). After the completion of the incubations, chambers were left in place until the following low tide, when they were removed. The area of sediment enclosed by each chamber was finger-ploughed (Thrush et al. 2006) to check that there were no large (>5mm) invertebrates present within treatments. In rare cases where invertebrates were found, these replicates were removed from analyses.

Incubations in old and new sediments were repeated in September 2011 at Discharge, Humphreys and Heron following the same protocol. During this sampling

period, nutrient samples were not collected. In December 2011, incubations were repeated at Humphreys and also done at Heathcote. This included the analysis of oxygen flux in the field, the collection of nutrient samples and the collection of BMA samples. Across all sites and sampling dates, the decline in oxygen in dark chambers was generally less than 20%. Due to logistical constraints (university shut-down due to the earthquake and no access to liquid nitrogen or specialised sampling equipment), BMA samples were not able to be collected in the earlier sampling periods. During these earlier sampling periods, however, visual observations of levels of BMA biomass on old and new sediments at each site were recorded and photographs taken to allow for comparisons among sites and sampling periods. Samples of BMA collected in December 2011 were done using a contact core, a simple bowl-shaped aluminium sampling device (internal diameter 2.5cm) with a 2mm high cavity on its bottom side (designed by Honeywill & Hagerthey and first cited in Ford and Honeywill (2002)). Contact cores were gently pushed into the sediment until the bottom of the metal bowl was flush with the surface of the sediment and liquid nitrogen was poured into the top of the bowl. Once the liquid nitrogen had evaporated, and the 2mm of sediment beneath the contact core was frozen, the contact core (+ frozen sediment) was removed from the surrounding sediment and a sharp flat knife used to scrape the frozen sediment until it was flush with the core. The resulting disc of sediment was removed from the contact core, wrapped in labelled tin foil and placed temporarily in liquid nitrogen before being stored at -80°C, pending analysis.

Sediment composition data (grain size and organic content) was collected for old and new sediments in April 2011, September 2011 and December 2011 at all sampled sites (and has been presented in *Chapter 3*).

5.2.2. Laboratory experiment

To examine the effects of three common, functionally diverse macrofauna present in the Avon-Heathcote Estuary on ecosystem functioning in old and new sediments, a laboratory experiment was done under controlled conditions using a tidal flow-through system. The system consisted of 36 plastic containers (“aquaria”), each of which could contain a 7.6cm (internal diameter) x 9cm (height) sediment core (Fig. 5.2). Each aquarium was supplied with seawater from one of 12 10L buckets, with each bucket supplying water to three aquaria. Seawater was collected from the

estuary mouth on an incoming tide and, as such, had relatively low nutrient levels. Light was supplied by Philips HPI-T 400W lights, with a diffuser placed underneath, providing a light intensity of 200-300µmolm^{-2}s^{-1}. White PVC sheets surrounded the experimental setup to ensure that light did not escape. Light and tidal cycles were programmed to the time of year and followed ambient patterns for the Avon-Heathcote Estuary. During low tide, the pump was switched off and water drained from the cores via holes drilled in the side of the cores directly above the sediment surface.

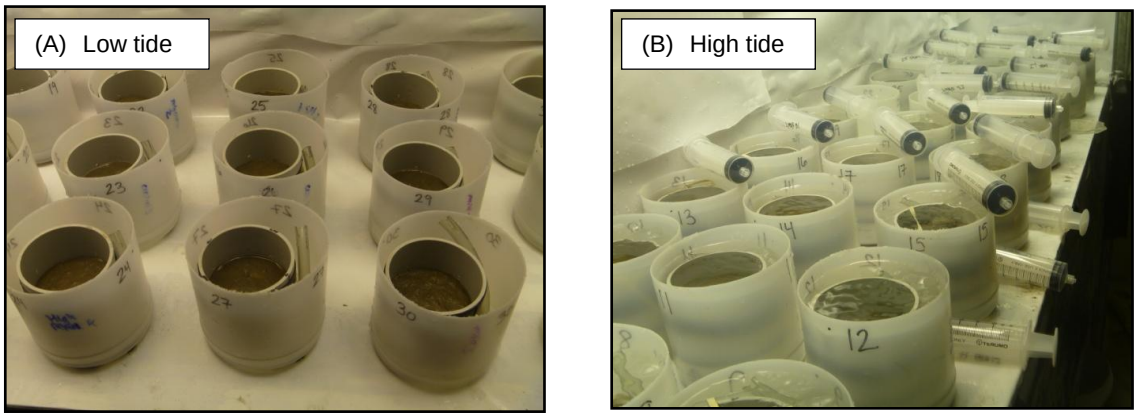

Figure 5.2. Mini-aquaria used to hold the cores in the laboratory experiment shown during low (A) and high (B) tide.

In May 2012, 32 sediment cores, as described above, were collected from areas of old (16 cores) and new (16 cores) sediment at Humphreys. All cores were taken from areas of approximately the same BMA cover (Chl *a* data from the control cores at the end of the experiment showed that there was no significant difference in Chl *a* concentration between cores taken from old and new sediments indicating that there was no/little difference initially). Care was also taken to avoid collecting cores from areas with fauna (i.e., where there were crab holes and/or obvious invertebrates). The advantage of collecting the cores at Humphreys was that the sediments at this site were relatively devoid of fauna (see *Chapters 2* and *3*) so collecting cores with unwanted invertebrates was not a major issue. Cores were filled with 5cm (height) of sediment and a PVC cap was placed on the bottom of each core. Once back in the laboratory, cores were placed in aquaria with light/dark and tidal cycles and left to acclimate for 24h. The allocation of cores to aquaria was randomly determined. Each day the water was changed in the flow-through system and F2 media was added to the seawater to help maintain BMA and invertebrate

nutrition. After two days (on “day 2”), initial incubations were performed on all cores. These were done prior to the treatments being established to ensure there were no significant differences among the cores and to identify any cores that may contain hidden invertebrates or have a different BMA biomass. To perform the incubations, the drainage holes in the sides of the cores were covered using a thick elastic band, and the top of the cores were covered with clear Perspex lids. A HACH HQ 30d probe was used to take initial and final (after 20 minutes – the short incubation time was due to the small size of the chambers) measurements of oxygen levels within each core under light conditions. The lights were then turned off and, after a 30 minute acclimation period, the incubation procedure was repeated.

After the initial incubations on day 2, treatments were established. There were three invertebrate treatments that were established in both old and new sediments: *Austrohelice*, *Austrovenus* and *Amphibola*, each containing one individual of the specified species. Control treatments (no invertebrates added) were also identified. There were four replicates of each treatment in each sediment type, providing a total of 32 experimental cores within the experiment. On days 4, 6 and 8, cores were incubated in the light and the dark (at high tide, as per the above procedure) and oxygen readings were taken. On day 6, water samples were also collected during the incubations and these were analysed for NH_4-N and NO_x-N and PO_4^{3-} to determine levels of nutrient flux. On day 8, after the final incubation, animals were removed from treatments and one contact core was taken from each core for Chl *a* analysis. A surface sediment scraping was also taken from each core for the analysis of organic content and grain size.

5.2.3. Laboratory analyses

Water samples were analysed for ammonium (NH_4-N), nitrate/nitrite (NO_x-N) and phosphate (PO_4^{3-}) using a spectrophotometer. Standard procedures were followed (NH_4-N as per Koroleff (1983), NO_x-N as per Parsons (1984) and PO_4^{3-} as per Koroleff (1983)).

Chl *a* samples were first freeze-dried for three days to remove moisture as Buffan-Dubau and Carman (2000) found that pigment recovery was nearly three times higher in sediments that were freeze-dried compared to those that were not. Chl *a* was then extracted using a modified version of the methods presented by Sartory and Grobbelaar (1984). Briefly, 10ml of 90% ethanol was added to 2g of

sediment from each sample and vials were shaken for 10s. Lids were then loosened slightly and the vials placed in an 80°C water bath for 10 minutes. Vials were removed from the water bath and when cool enough to handle, lids were tightened and the vials shaken well for 10s. Samples were then left in the dark for at least 12h. After this, samples were shaken well for 10s and left in the dark for at least another 3h to allow the sediments to settle. For each sample, the liquid (containing the chlorophyll) was then carefully poured into a curvette. Each curvette was placed in a spectrophotometer to assess the concentration of Chl *a* at 663 and 750nm wavelengths. After the first reading, samples were removed from the spectrophotometer and three drops of 1mol HCl were added to each sample. Parafilm was placed over the curvette to allow it to be inverted to mix and, after 1 minute, a second reading was taken for the sample. Chlorophyll *a* levels were calculated according to Lorenzen (1967), with a correction for phaeopigment content.

Sub-samples of sediment from each treatment were dried (60°C for 3d) and then combusted (550°C for 5h), enabling the calculation of the organic content of each sample. Additional sub-samples were dried at 60°C for 3d and wet-sieved through a series of sieves (500µm, 250µm, 125µm, 63µm) to determine the fraction of sediment in each size class (250-500µm = medium sand, 125-250µm = fine sand, 63-125µm = very fine sand, <63µm = silt) (Wentworth 1922).

5.2.4. Statistical analyses

For the *in situ* data, general linear models (GLMs) were used to examine differences between sediment types (fixed; 2 levels: old and new) for each response variable at each site at each sampling date. The response variables were: O_2 flux dark (Total Oxygen Utilization (TOU)), O_2 flux light (Net Primary Production (NPP)), O_2 flux light–flux dark (Gross Primary Production (GPP)), NH_4-N flux dark (NH_4-N availability), NH_4-N flux light, NH_4-N flux dark – flux light (photosynthetic uptake of NH_4-N), NO_x-N flux dark (NO_x-N availability), NO_x-N flux light, NO_x-N flux dark – flux light (photosynthetic uptake of NO_x-N), PO_4^{3-} flux dark (PO_4^{3-} availability), PO_4^{3-} flux light, PO_4^{3-} flux dark – flux light (photosynthetic uptake of PO_4^{3-}), Chl *a* and GPP/Chl *a* (photosynthetic efficiency). For O_2, NH_4-N, NO_x-N and PO_4^{3-} flux under dark conditions, additional GLMs were run that included site (fixed) and sampling date (random), as well as sediment type, as factors in the analysis. Site was considered a fixed factor due to the eutrophication and disturbance gradients spanning the

different sampling areas. Site and sampling date were not included as factors in the analysis of light chamber results (or any results calculated using light chamber measurements) as there were differences in light levels among sites and sampling dates (caused by differences in seasonal sunlight intensity and water turbidity despite all incubations occurring on sunny days) and these affected absolute values. For example, Hobo® data loggers deployed during light incubations at Humphreys and Heathcote occurring at the same time on the same (sunny) day, recorded within-chamber light levels of 437mmol$m^{-2}s^{-1}$ at Heathcote and 96mmol$m^{-2}s^{-1}$ at Humphreys. Where necessary, data were log-transformed to fulfil the assumptions of the model and where Cochran's test for homogeneity of variances remained significant after data transformation, p-values were made more conservative by reducing the significance threshold from 0.05 to 0.01 (Underwood 1997). Tukey post-hoc tests were performed to examine the direction of significant relationships.

Data from the laboratory experiment were analysed similarly to the field experiment, with the exclusion of the factor "site" and the inclusion of the factor "day" (random; 4 levels: day 2, 4, 6, 8) for oxygen flux. Grain size and organic content data were also analysed using GLMs. All GLMs were done using STATISTICA 7.

5.3. Results

5.3.1. *In situ* sampling

Individual analysis for each site at each sampling date showed no significant differences in TOU between old and new sediments in all instances (Fig. 5.3A). There were, however, significant differences in TOU among sites in April 2011 ($F_{2,18}$=6.98 p=0.0057). Sediment type ($F_{1,18}$=1.80 p=0.20) and the site x sediment type interaction effect ($F_{2,18}$=0.14 p=0.87) were not significant. During this initial sampling period, TOU was highest in sediments at Discharge. In September 2011, there were also significant differences in TOU among sites but efflux at Humphreys was now the highest. Analysis of TOU for individual sites across sampling dates showed no significant changes over time (all p>0.05) except for at Discharge, where there was significant reduction in TOU between April and September 2011 ($F_{1,14}$=4.96 p=0.043).

Net primary production varied among sites, between old and new sediments and through time (Fig. 5.3B). Discharge sediments were initially in net respiration (April 2011) and barely produced by September 2011. Heron and Heathcote had

values of NPP that were close to zero, particularly in old sediments. Although not significant, new sediments had greater average productivity than old sediments at Heron in September 2011 and at Heathcote in December 2011. At Humphreys, NPP was significantly higher in new versus old sediments in April 2011 ($F_{1,6}$=14.04 p=0.0095) with both sediment types in net production. In September and December 2011, however, both old and new sediments were in net respiration at this site.

Gross primary production was greatest at Humphreys and almost always higher in new sediments than in old sediments (Fig. 5.3C) particularly at Discharge ($F_{1,6}$=8.40 p=0.027) and Humphreys ($F_{1,6}$=4.4 p=0.081) in April 2011. There was a reduction in GPP in old and new sediments at Humphreys between April 2011 and September/December 2011.

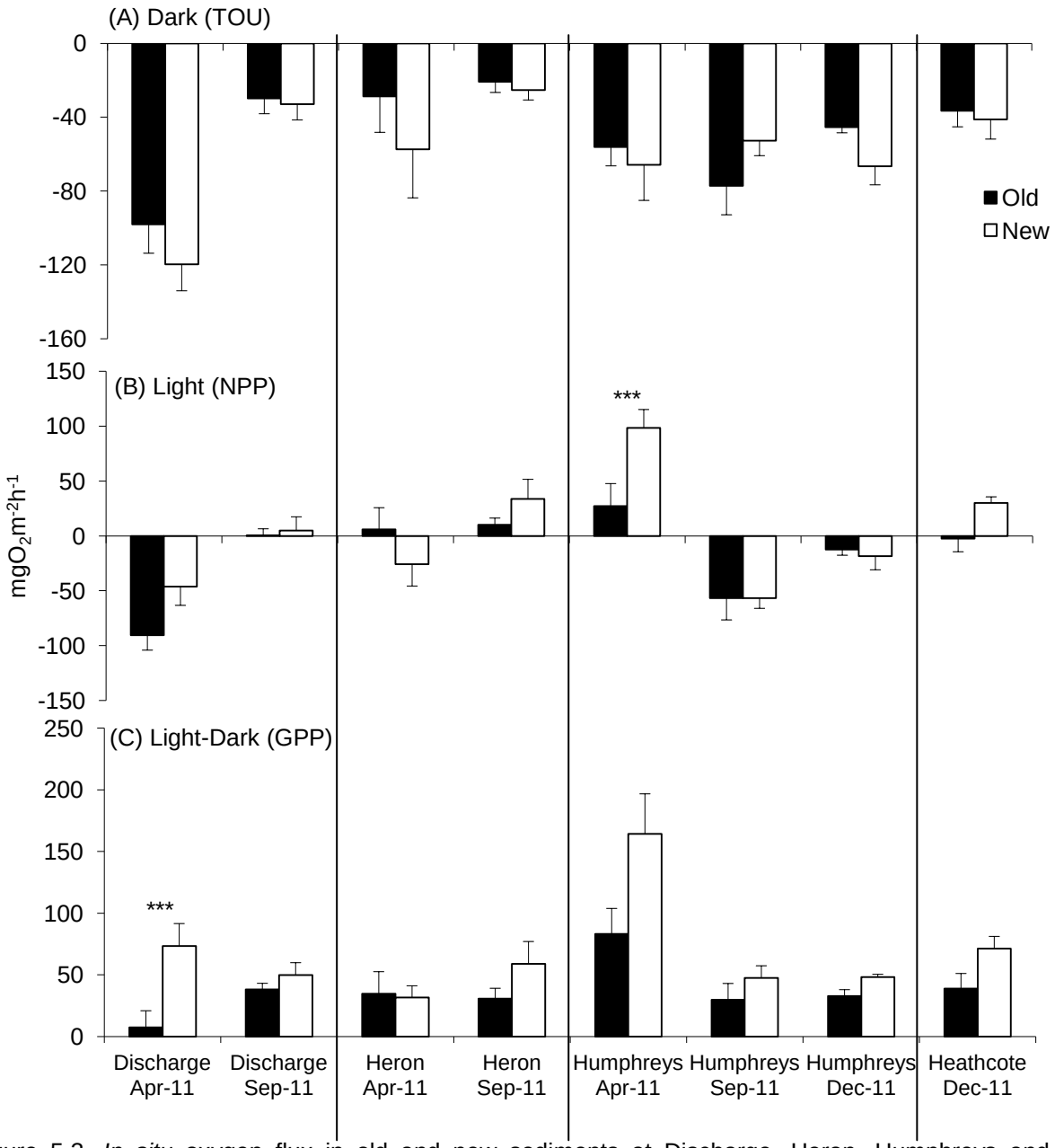

Figure 5.3. *In situ* oxygen flux in old and new sediments at Discharge, Heron, Humphreys and Heathcote on various sampling occasions in 2011 after the February earthquake under dark (A) and light (B) conditions. Light-Dark flux is shown in C. N=4. *** =old and new sediments are significantly ($p<0.05$) different.

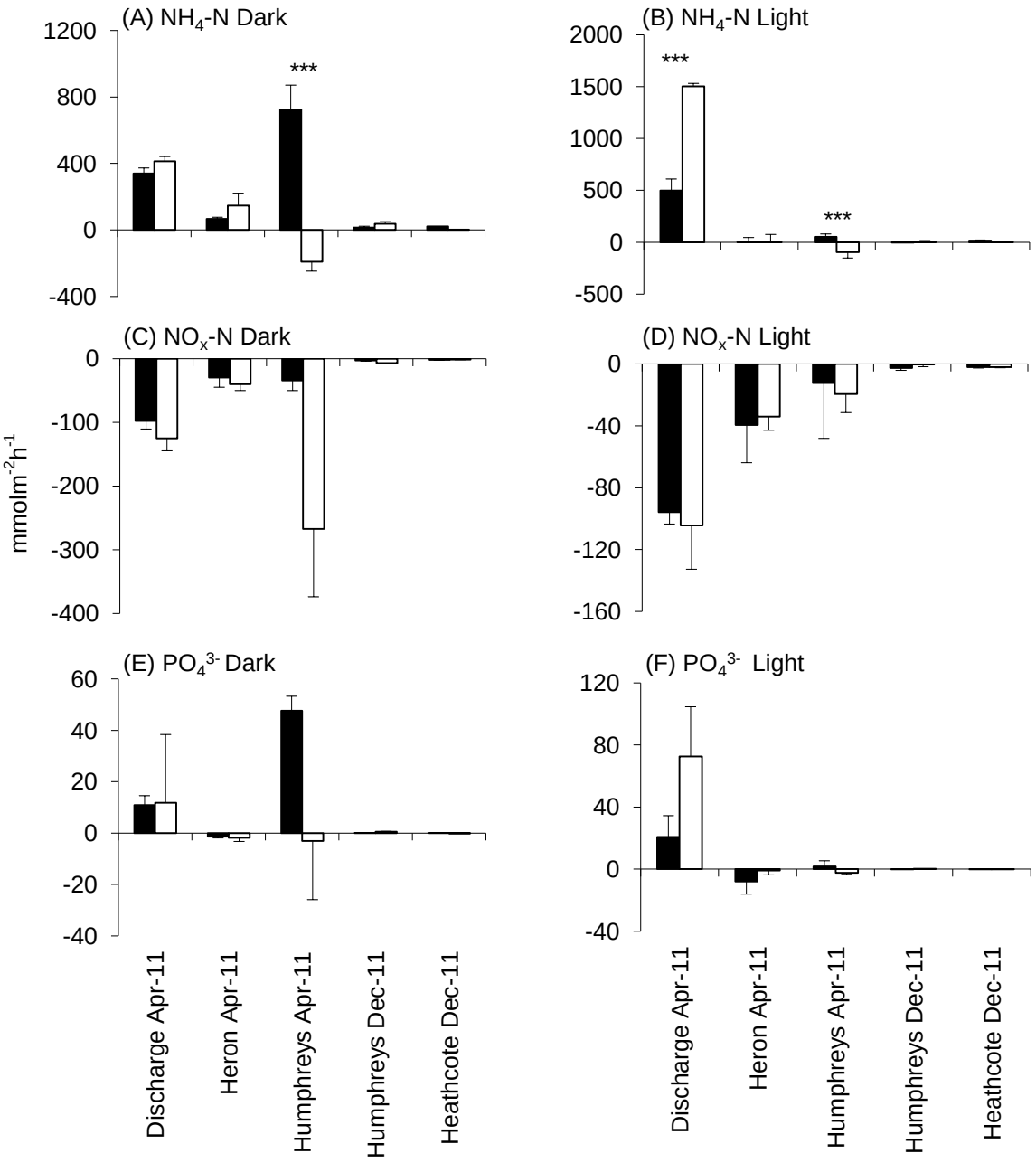

Figure 5.4. *In situ* flux of NH_4-N, NO_x-N and PO_4^{3-} in old and new sediments at Discharge, Heron, Humphreys and Heathcote in April 2011 and December 2011 after the February 2011 earthquake. Dark flux indicates nutrient available for uptake. N=4. *** =old and new sediments are significantly ($p<0.05$) different.

Under dark conditions in April 2011 there were significant differences in NH_4-N flux (NH_4-N availability) among sites ($F_{2,11}=5.85$ $p=0.019$), between sediment types ($F_{1,11}=15.67$ $p=0.0022$) and the site x sediment type interaction effect was significant ($F_{2,11}=27.79$ $p<0.001$). During this initial sampling period, dark NH_4-N flux in old sediments was lowest at Heron and highest at Humphreys (Fig. 5.4A). In new sediments, dark NH_4-N flux was highest at Discharge and lowest at Humphreys.

Individual analysis for each site in April 2011 showed no significant differences in dark NH_4-N flux between old and new sediments at Discharge and Heron, but that NH_4-N flux at Humphreys was significantly higher in old versus new sediments ($F_{1,4}$=34.43 p=0.0042). In December 2011, however, there were no significant differences between old and new sediments at Humphreys with both sediment types showing low levels of NH_4-N efflux.

Under light conditions, individual analysis for each site at each sampling date showed that NH_4-N flux was significantly higher in new sediments than in old sediments at Discharge in April 2011 and significantly higher in old sediments than in new sediments at Humphreys in April 2011 (Fig. 5.4B).

Under dark conditions there were no significant effects of site, sediment type or their interaction on NO_x-N flux. All fluxes were negative indicating the influx of NO_x-N into the sediment at all sites on all sampling dates (Fig. 5.4C). Individual analysis for each site at each sampling date showed no significant differences in light NO_x-N flux between old and new sediments (Fig. 5.4D).

Under dark conditions, there were no significant effects of site, sediment type or their interaction on PO_4^{3-} flux but relatively high levels of efflux occurred in old sediments at Humphreys (Fig. 5.4E). Under light conditions, individual analysis for each site at each sampling date showed no differences in PO_4^{3-} flux between old and new sediments (Fig. 5.4F).

There were large variations in Chl *a* concentration among sites and between old and new sediments at Humphreys based on visual observations and photographic records for April and September 2011, summarised in Table 5.1. Chl *a* concentration was highest at Humphreys, particularly in old sediments and consistently low in both sediment types at Heron. For Chl *a* samples collected at Humphreys and Heathcote in December 2011, Chl *a* concentrations in old and new sediments were significantly higher at Humphreys than at Heathcote ($F_{1,11}$=8.50 p=0.014) (Fig. 5.5A). There were no differences in Chl *a* concentration between sediment types ($F_{1,11}$=0.43 p=0.53) and the site x sediment type interaction effect was not significant ($F_{1,11}$=0.0087 p=0.93). Chl *a* concentration in old and new sediments at Humphreys ranged from 27.9 - 31µg/g of sediment compared to 6.2 - 7.3µg/g of sediment at Heathcote.

To examine differences in photosynthetic efficiency among sites and between sediments types GPP/Chl *a* was calculated. Photosynthetic efficiency was

significantly higher in old and new sediments at Heathcote than in old and new sediments at Humphreys in December 2011 ($F_{1,10}$=19.70 p=0.0013). There were no significant differences in photosynthetic efficiency between sediment types ($F_{1,10}$=0.16 p=0.69) and the site x sediment type interaction effect was not significant ($F_{1,10}$=0.00003 p=0.10). Photosynthetic efficiency in old and new sediments at Humphreys ranged from 1.9 – 2.2 compared to 10.7 – 11.8 at Heathcote (Fig. 5.5B). Scatterplots showed that photosynthetic efficiency was very low at Chl *a* concentrations beyond ~13 µg/g of sediment in old and new sediments, probably due to increased shading and competition for light and nutrients at high BMA densities (Fig. 5.6).

Table 5.1. Relative Chl *a* concentrations based on visual observations of BMA biomass on old and new sediments at Humphreys, Discharge and Heron in April and September 2011

	Humphreys		**Discharge**		**Heron**	
	Old	**New**	**Old**	**New**	**Old**	**New**
Apr-11	Very high	High	Some	Some	Low	Low
Sep-11	Very high[1]	Some[2]	Some	Some	Low[3]	Low[4]

[1] 120±20 µg/g sediment (simultaneous study by Hutt (2012))
[2] 13±7 µg/g sediment (simultaneous study by Hutt (2012))
[3] 10±1 µg/g sediment (at nearby Plover site (simultaneous study by Hutt (2012))
[4] 9±0.5 µg/g sediment (at nearby Plover site (simultaneous study by Hutt (2012))

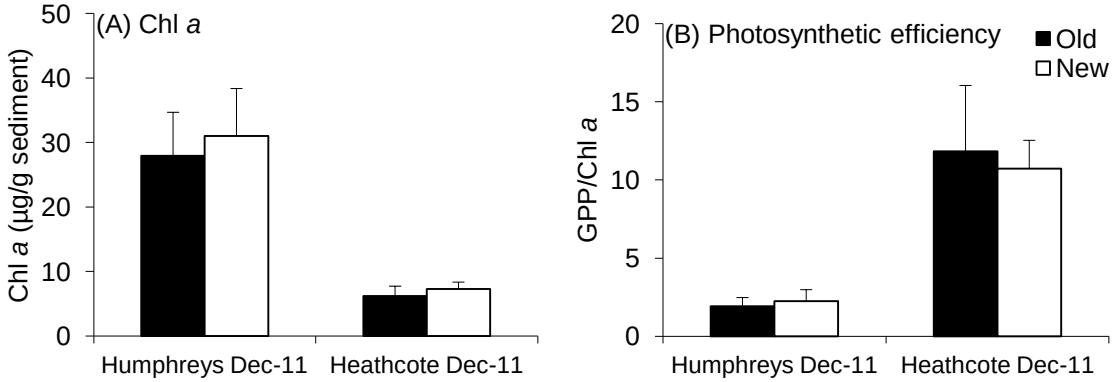

Figure 5.5. Chl *a* concentration (A) and photosynthetic efficiency (GPP/Chl *a*) (B) in old and new sediments at Humphreys and Heathcote in December 2011. N=4.

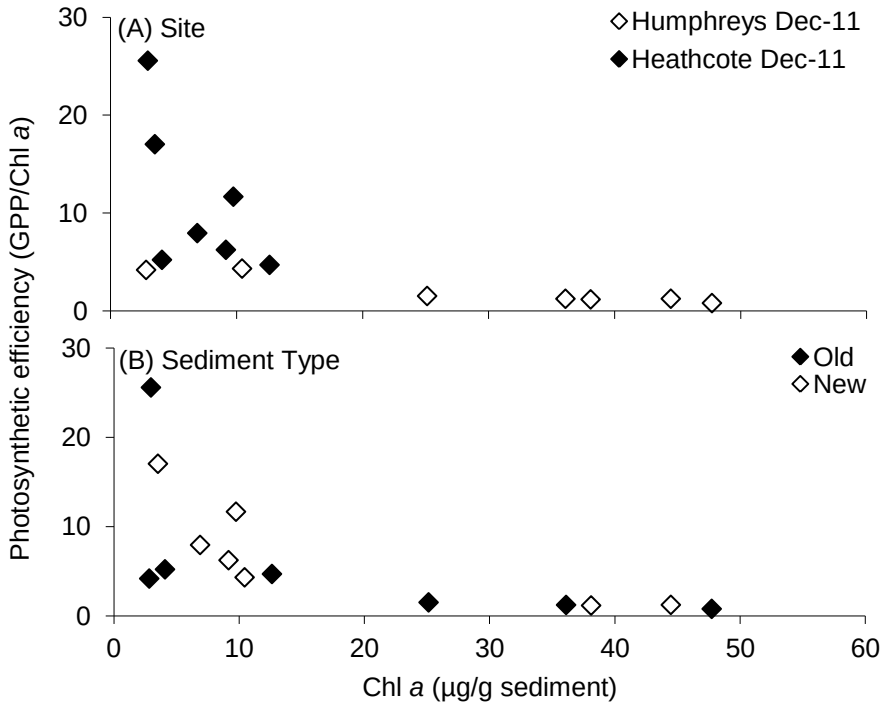

Figure 5.6. Chl *a* concentration versus photosynthetic efficiency (GPP/Chl *a*) at Humphreys and Heathcote in December 2011 in old and new sediments plotted by site (A) and sediment type (B).

5.3.2. Laboratory experiment

Invertebrate type did not have a significant effect on TOU but there was a significant effect of day ($F_{3,96}$=5.26 p =0.0021) that was driven by changes in flux after the addition of invertebrates (after the day 2 incubations). Although not significant, the largest changes in average TOU occurred in the *Amphibola* treatment (Fig. 5.7A,D). There were no changes in TOU in the controls over the course of the experiment. There was a significant effect of day ($F_{3,96=}$14.48 p<0.0001), invertebrate type ($F_{3,96}$=53.09 p<0.0001) and the day x invertebrate type interaction effect ($F_{9,96}$=5.99 p<0.0001) on oxygen flux under light conditions. These effects were driven by the significant reduction in oxygen flux in the *Austrohelice* and *Amphibola* treatments after the addition of invertebrates after the day 2 incubations. The addition of *Austrovenus* did not change oxygen flux under light conditions (NPP) and, across all invertebrate types, there were no changes from days 4-8 (Fig. 5.7B,E). There were significant effects of day ($F_{3,96}$=6.69 p=<0.001), invertebrate type ($F_{3,96}$=30.76 p<0.001) and the day x invertebrate type interaction effect ($F_{9,96}$=3.46 p<0.001) on GPP. In particular, the addition of *Austrohelice* and *Amphibola* resulted in a reduction in GPP, whereas the addition of *Austrovenus* caused a slight increase (although not

significant) in GPP (Fig. 5.7C,F). There were no differences in levels of GPP between old and new sediments for each invertebrate treatment and the control.

Invertebrate type had a significant effect on the flux of NH_4-N under dark ($F_{3,23}$=12.29 p<0.0001) and light ($F_{3,23}$=5.05 p=0.0078) conditions with *Austrohelice* > *Amphibola* > *Austrovenus* > control (Figs. 5.8A,B). There were no differences in the uptake of NH_4-N among treatments (Fig. 5.8C). High variability in the NO_x-N and PO_4^{3-} data sets meant that no significant differences were found for dark and light flux, and the photosynthetic uptake of these nutrients among treatments (Figs. 5.8D-I).

There were significant effects of sediment type ($F_{1,24}$=12.20 p=0.0019), invertebrate type ($F_{3,24}$=87.16 p<0.0001) and the interaction of these two factors ($F_{3,24}$=3.34 p=0.036) on Chl *a* concentration with *Austrohelice* < *Amphibola* < *Austrovenus*/control. There was a trend of higher Chl *a* concentrations in old sediments relative to new sediments, particularly for *Austrohelice* and *Amphibola* treatments (Fig. 5.9A). Photosynthetic efficiency (GPP/Chl *a*) did not differ significantly among any treatments. Values ranged from 11.4 – 20.9 (Fig. 5.9B).

There was a significant effect of sediment type on the percentage organic content of sediments ($F_{1,17}$=58.11 p<0.001) with higher levels occurring in old sediments. There was no effect of invertebrate type. The organic content of new sediments was around 1.5% whereas in old sediments, it was around 2.6% (Fig. 5.10). New sediments had a higher proportion of coarser grain sized particles than old sediments, but grain size did not differ significantly among invertebrate treatments (Table 5.2). For all invertebrate treatments, the mud (<63µm) content of old sediments was at least twice that of new sediments (Fig. 5.11).

Comparison of the photographs in Figs. 5.12 and 5.13 shows that the addition of *Austrohelice* to new sediments caused the sediment to become well mixed and piled in a heap whereas in old sediments, this species built one or several burrows. *Amphibola* noticeably reduced the abundance of BMA through grazing in both old and new sediments. The addition of *Austrovenus* did not appear to change the sediment surface in any obvious visual way and in some cases these individuals did not burrow, particularly in new sediments, indicating they may not have been exhibiting their normal behaviour.

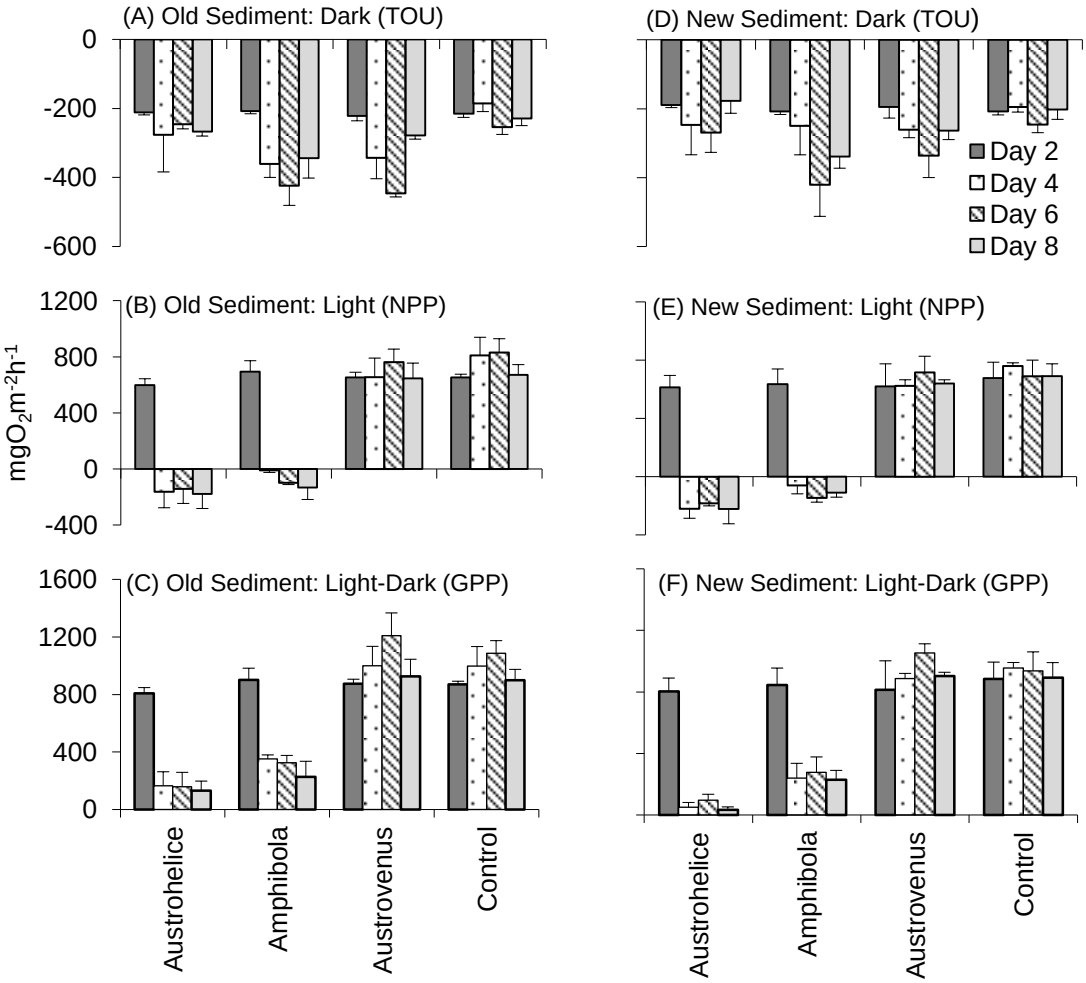

Figure 5.7. Oxygen flux in old (A-C) and new (D-F) sediments under dark (A,D) and light (B,E) laboratory conditions for different invertebrate treatments: *Austrohelice crassa*, *Amphibola crenata*, *Austrovenus stutchburyi* and the control at 2 day intervals over the 8 day experiment. Light-Dark flux (GPP) is shown in (C) and (F) for old and new sediments respectively. N=4. Note that invertebrates were added after the day 2 incubations.

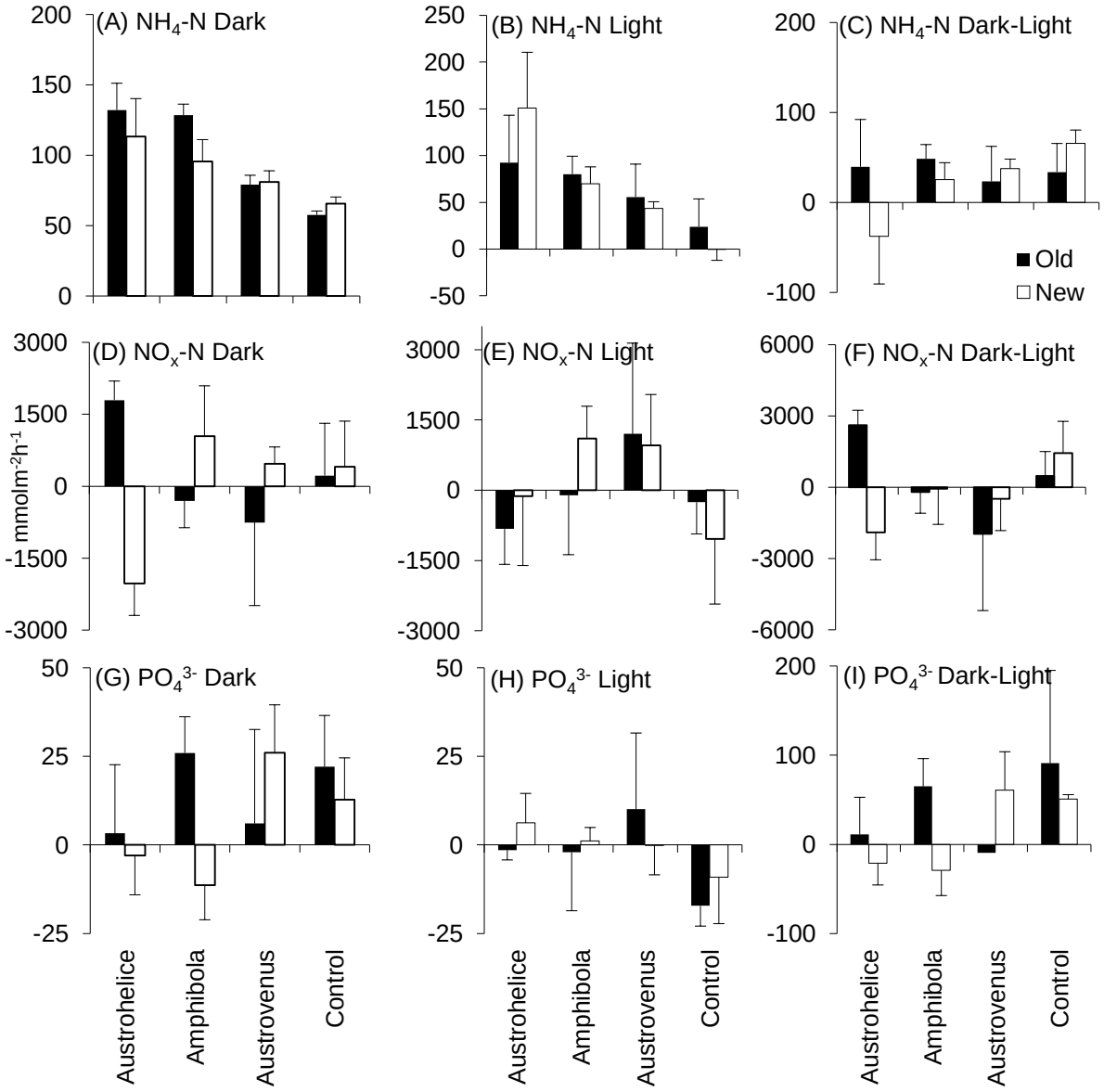

Figure 5.8. Flux of NH_4-N (A-C), NO_x-N (D-F) and PO_4^{3-} (G-I) under dark (A,D,G) and light (B,E,H) conditions in old and new sediments for different invertebrate treatments: *Austrohelice crassa*, *Amphibola crenata*, *Austrovenus stutchburyi* and the control. Uptake (C,F,I) is dark – light flux. N=4. Note the differences in y-axis scales. Measurements of nutrient flux were taken on day 6 of the experiment.

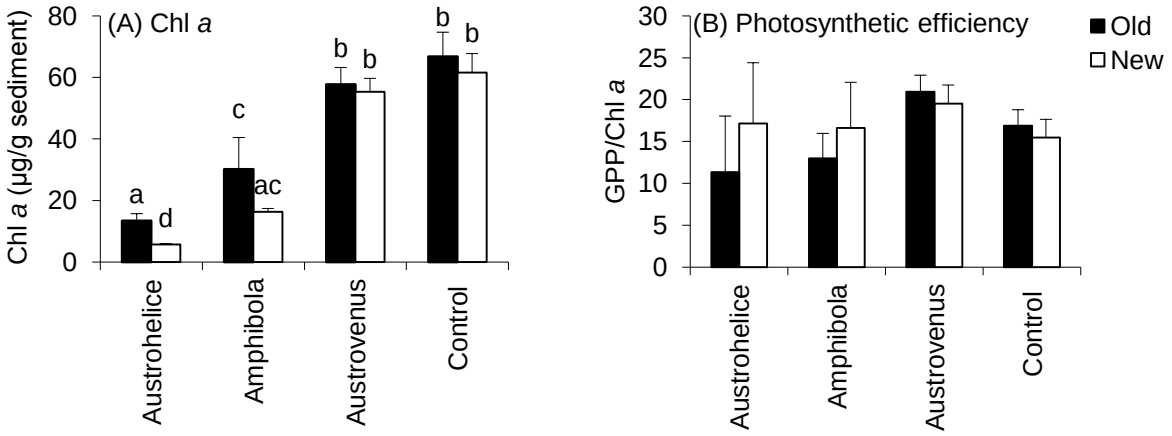

Figure 5.9. Chl *a* concentration (A) and photosynthetic efficiency (GPP/Chl *a*) (B) in old and new sediments at the completion of the laboratory experiment (after day 8 incubations) for different invertebrate treatments: *Austrohelice crassa*, *Amphibola crenata*, *Austrovenus stutchburyi* and the control. For (B), GPP values from Day 6 are used for the calculation. Letters denote treatments that are significantly different.

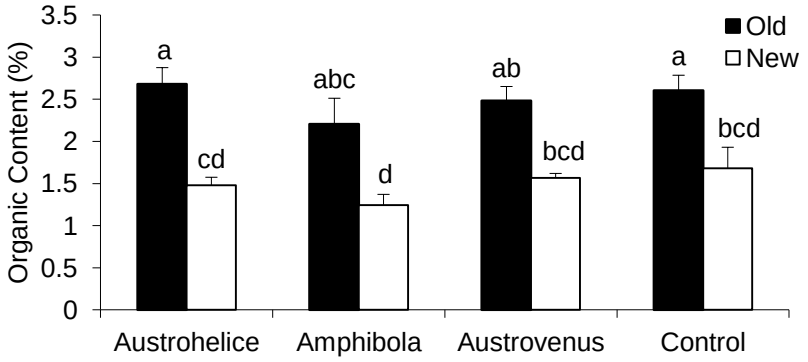

Figure 5.10. Percentage organic content in old and new sediments for different invertebrate treatments: *Austrohelice crassa*, *Amphibola crenata*, *Austrovenus stutchburyi* and the control at the completion of the laboratory experiment. Letters denote treatments that are significantly different. N=3-4.

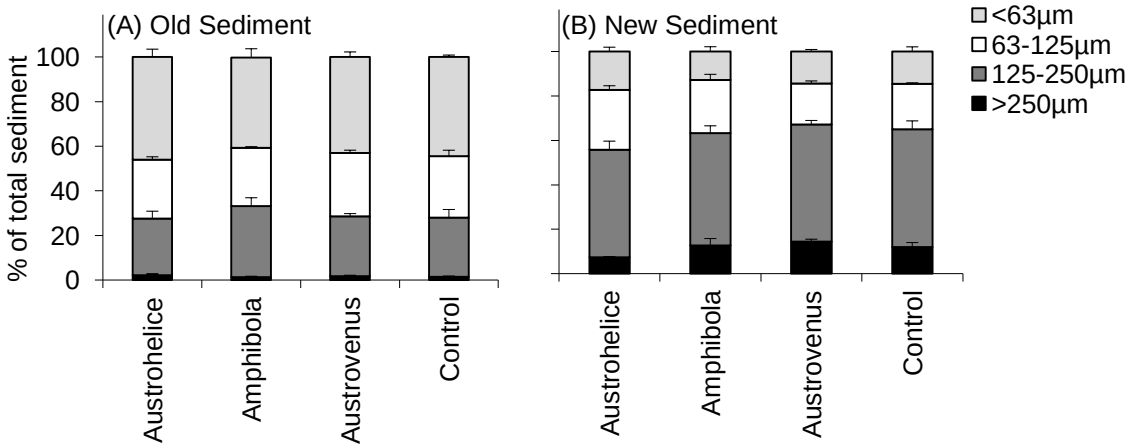

Figure 5.11. Percentage of different size classes of sediment grains in old (A) and new (B) sediments for different invertebrate treatments: *Austrohelice crassa*, *Amphibola crenata*, *Austrovenus stutchburyi* and the control at the completion of the laboratory experiment. N=3-4.

Table 5.2. General linear model analysis showing differences in the grain size of surface sediments across two sediment types (old and new) and four invertebrate types (*Austrohelice crassa*, *Amphibola crenata*, *Austrovenus stutchburyi* and the control) at the completion of the laboratory experiment. *Cochran's C still significant after log-transformation so significance reduced to 0.01. N=3-4.

Grain Size (µm)	Sediment Type			Invertebrate Type			Sediment Type* Invertebrate Type		
	DF	F	p	DF	F	p	DF	F	p
<63	1,19	137.82	**<0.0001**	3,19	1.16	0.35	3,19	0.38	0.77
63-125	1,19	4.66	0.044*	3,19	2.005	0.15	3,19	2.50	0.09
125-250	1,19	118.32	**<0.0001**	3,19	0.74	0.54	3,19	1.16	0.35
>250	1,18	209.24	**<0.0001**	3,18	0.87	0.48	3,18	3.37	0.04*

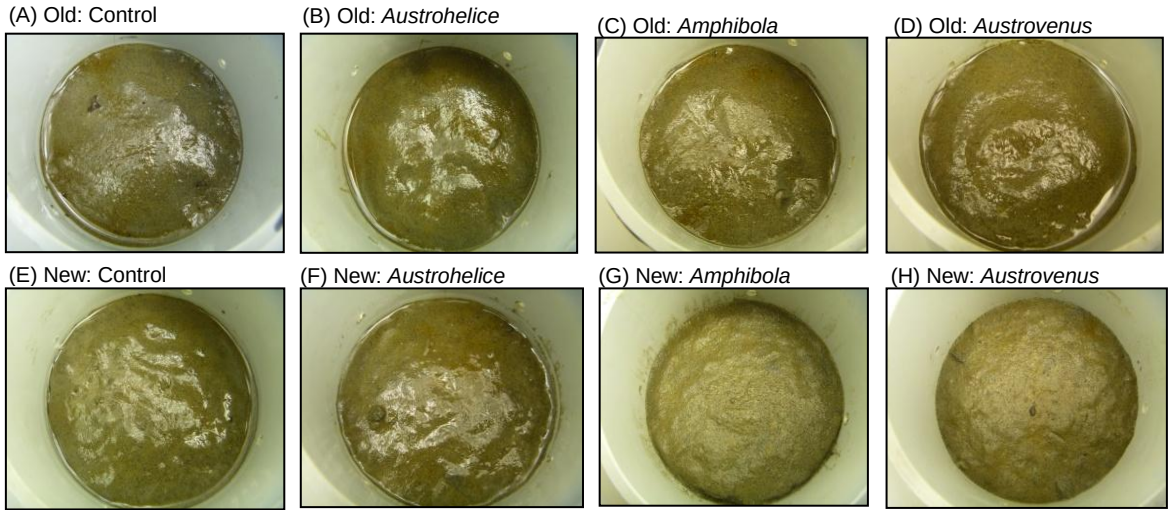

Figure 5.12. Photographs of old sediment (A-D) and new sediment (E-H) cores used in the laboratory experiment on day 2, prior to the addition of invertebrates to their respective treatments (control, *Austrohelice crassa*, *Amphibola crenata*, *Austrovenus stutchburyi*).

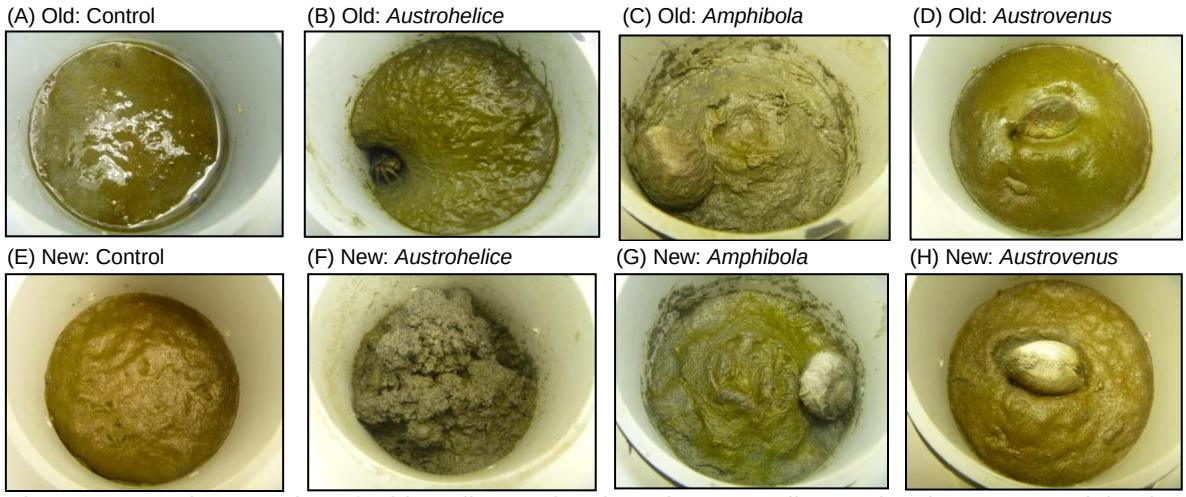

Figure 5.13. Photographs of old sediment (A-D) and new sediment (E-H) cores used in the laboratory experiment on day 4, after the addition of invertebrates to their respective treatments (control, *Austrohelice crassa*, *Amphibola crenata*, *Austrovenus stutchburyi*) after the day 2 incubations.

5.4. Discussion

5.4.1. In situ ecosystem functioning: Old versus new sediments

There were some clear differences in GPP between old and new sediments but the magnitude of these differences varied among sites and was related to the eutrophication gradient within the estuary. Within site variability was much higher at the eutrophic sites than at the clean site and interestingly, GPP was higher in new sediments than in old sediments in these areas. This is probably because new sediments are much coarser than the old sediments, enabling enhanced light penetration and backscatter that will allow light to reach BMA deeper in the sediment thus enabling increased levels of photosynthesis (Paterson 1998). The increased permeability of new sediments also allows for the enhanced vertical migration of BMA and the enhanced transport of oxygen and nutrients, all of which can increase levels of primary production. Chlorophyll *a* measurements reported by Hutt (2012) in September 2011 at Humphreys showed that Chl *a* concentration in old sediments was approximately 10 times greater than that in new sediments. Thus it appears that although there is generally a positive relationship between BMA biomass and GPP (many studies report a positive relationship between Chl *a* concentration and production (e.g., Asmus and Asmus 1985, Andersen and Kristensen 1988, Webb and Eyre 2004)), at higher levels of Chl *a* concentration (i.e., in old sediments), individual BMA are increasingly competing with each other for light and nutrients (consistent with Morrisey 1988). Also, there is the probability that BMA at the bottom of a thick microalgal mat may be shaded out. Consequently, it appears that BMA in new sediments have an increased photosynthetic efficiency (>GPP/unit Chl *a*). It is also acknowledged that species shifts in BMA communities can alter levels of productivity (Falkowski and Kiefer 1985) and that BMA community composition can vary as a function of sediment composition, in particular grain size (Round 1971, Heip et al. 1995, Paterson and Hagerthey 2001) and ammonium concentration (Peletier 1996, Underwood et al. 1998) which may have been the case in the Avon-Heathcote Estuary although it is likely that the effect of these factors would be relatively minimal in comparison to the effects of light and BMA biomass.

At Humphreys, the most eutrophic site, there is a large amount of re-suspension of the fine muddy sediments making water turbidity high in these areas. This reduces light levels in the water column and consequently, photosynthesising BMA in surface sediments rarely, if ever, reach P_{max} even on bright days in summer

(Table 5.3). Because differences in light intensity among sites affected absolute values, site differences in GPP were not analysed in this study. But, it is interesting to note that regardless of the highly compromised light environment at Humphreys, GPP was still high, particularly in new sediments. This is driven by the higher biomass of BMA and the increased amounts of legacy ammonium stored in the sediments that is available for uptake by BMA (note that nutrient uptake also occurs via denitrification and nitrification by bacteria) which can increase photosynthetic efficiency. In contrast to the eutrophic sites, sediments at Heron, a relatively clean site on the eastern side of the estuary, are sandier with less organic matter and fewer legacy nutrients. Despite the increased water clarity (i.e., P_{max} reached) and coarser sediments (enabling deeper light penetration into the sediments) at this site, GPP was low compared to at the eutrophic sites (Table 5.3). This is because of the relatively low BMA biomass and ammonium efflux from the sediments, compared to at the eutrophic sites, both of which can reduce productivity. At this cleaner site, there was less variability in productivity and nutrient efflux between old and new sediments because sediment characteristics were more similar.

Table 5.3. Synthesis of site characteristics for Humphreys, Discharge and Heron and their associated relative levels of BMA biomass (Chl *a* concentration), total oxygen utilisation (TOU), net primary production (NPP), gross primary production (GPP) and NH_4-N efflux in April 2011 after the February 2011 earthquake. P_{max} = the maximum potential photosynthetic rate per individual. Net resp. = net respiration; Net prod. = net production.

	Sediment Type	Humphreys	Discharge	Heron
Eutrophication Status		Very High	High	Low
P_{max} reached?		Unlikely	Unlikely	Likely
Turbidity		High	High	Low
BMA Biomass	**Old**	Very High	Some	Low
	New	High	Some	Low
TOU	**Old**	Some	High	Some
	New	Some	High	Some
NPP	**Old**	Net resp.	Net resp.	Net prod.
	New	Net resp.	Net resp.	Net resp.
GPP	**Old**	Lower	Low	Low
	New	Higher	High	Low
NH_4-N Efflux	**Old**	Very High	High	Low
	New	Influx	High	Low

The capping of areas of old sediments with new sediments at the most eutrophic site (Humphreys) significantly reduced the efflux of legacy nutrients. For example, two months after the February 2011 earthquake, the efflux of ammonium (and phosphate) at Humphreys was 3-4 times greater in old sediments than in new sediments. In fact, over the incubation period under dark conditions, a net influx of ammonium, rather than an efflux, occurred in new sediments. This indicates that there were very low amounts of ammonium in new sediments and that these sediments were probably taking up ammonium due to high quantities of this nutrient in the surrounding water. This was due to the input of large amounts of raw sewage (high in ammonium) to the estuary after the February 2011 earthquake (which continued until October 2011). Over time, nutrient efflux in old and new sediments became similar with low levels occurring in December 2011. This is due not only to the mixing of old and new sediments, but also the development and growth of bacterial and microalgal communities in those sediments. Consequently, both the short (2 month) and longer term (10 month) results indicate that the introduction of new sediments has most likely accelerated the recovery of the estuary by burying large portions of eutrophic sediments. This finding represents a large-scale natural capping event that seems to have produced results similar to small-scale remediative practices that reduce nutrient and/or elemental fluxes from eutrophic and degraded sediments. For example, Azcue et al. (1998) found that capping of sediments in Hamilton Harbour, Canada with a clean 35cm layer of medium-to-coarse sand significantly reduced the vertical flux of trace elements. Additionally, Kim et al. (2007) reported that sand-capping effectively reduced total phosphorus release from phosphorus-rich sediment in a Central Korean lake. In my study the capping of sediments was, however, a little different as it was extremely patchy and occurred on a microscale resulting in considerable within site variation particularly at the eutrophic sites. Over time, there was undoubtedly cross-contamination between old and new sediment patches.

5.4.2. Effects of large invertebrates on ecosystem functioning

Invertebrates altered levels of primary production and nutrient flux but effects varied among species. This finding is in line with an increasing literature that promotes the important role of functional diversity, as opposed to biodiversity, in ecosystem functioning. In all cases, the change in primary production that occurred within the

first 48 hours (i.e., between days 2 and 4) of adding invertebrates did not alter for the remainder of the experiment (from days 4-8). This indicates that invertebrates can have a rapid and immediate effect on their environment but it is also likely that the results were influenced by the small size of the cores used in the experiment in which a small volume/surface area of sediment could be altered rapidly by invertebrates. Effects occurred both through bioturbation and grazing, reflecting the different functional aspects of the invertebrates.

The addition of *Austrohelice* had the greatest impact on GPP, reducing it by approximately 80% in old sediments and by >90% in new sediments. This was correlated well with an 80% to 90% difference in Chl *a* concentration between control and *Austrohelice* treatments for old and new sediments respectively. Most studies report a positive relationship between Chl *a* concentration and production, reflective of the presence and production of microalgae (e.g., Asmus and Asmus 1985, Andersen and Kristensen 1988, Webb and Eyre 2004). Needham et al. (2011) also found *Austrohelice* to reduce BMA standing stock through consumption and reburial (via the construction and collapse of burrows). Interestingly, observations and photographs from my study showed very different burrowing behaviours of *Austrohelice* in the two sediment types, with crabs in new sediments mixing sediments and piling them in a heap over the whole sediment surface, whereas crabs in old sediments building only one or two burrows into the sediment and not altering the sediment surface as a whole. Similarly, Needham et al. (2011) also found *Austrohelice* to exhibit functional plasticity by switching to a vertical mixer in non-cohesive sediments due to the frequent collapse of burrows in sandier sediments. *Austrohelice* also increased the availability of NH_4-N (i.e., flux under dark conditions) which is probably due to the high bioturbation rates of these crab and their burrow building activity, resulting in greater NH_4-N efflux from the sediment. Needham et al. (2011) also found increased NH_4-N flux from the sediment with increased density of *Austrohelice*. These authors reported NH_4-N fluxes to be higher in muddier sediments where burrows and their microbial communities were most stable but in my study, no differences in NH_4-N flux between old and new sediments were found. This is probably due to the scale of those chambers and large differences in the number of burrows in mud versus sand. In contrast, the microcosms I used were small with one crab per microcosm.

Similar to *Austrohelice*, the reduction in GPP for *Amphibola* was also well correlated with a reduction in Chl *a* concentration which, in this case, was accounted for by the grazing activity of *Amphibola*. Interestingly, visual observations showed a large difference in BMA biomass in the first 48h after the addition of *Amphibola* that is consistent with the reduction in GPP over this time period. Over the remainder of the experiment, changes in BMA biomass were not visually noticeable and, accordingly, there was no significant change in GPP from days 4-8. It is unclear as to whether the reduction in BMA uptake by *Amphibola* was due to the reduced abundance of BMA (although there was still some that remained unconsumed) or a behavioural/physiological response to the experimental conditions. The trend of slightly higher levels of GPP in old versus new sediments was probably due to slightly higher Chl *a* concentrations in old sediments, rather than any effect of sediment type. Dark NH_4-N flux was also greater in *Amphibola* treatments, relative to the control, which, as *Amphibola* only interact with the surface sediment layers, was probably due to the production of faeces, as well as nitrogen release from surface sediments. Unlike *Austrohelice*, *Amphibola* did not appear to show any obvious form of functional plasticity between old and new sediments which is perhaps expected given this species lives on the surface. To the best of my knowledge, there are no other studies that examine the role of *Amphibola*, or any estuarine grazer species, on primary production which prevents comparisons with other literature. But, given the magnitude of change in primary production seen with the addition of *Amphibola*, this is perhaps a species, or functional group, that warrants further attention.

Unlike *Austrohelice* and *Amphibola*, *Austrovenus* did not alter GPP relative to the control. Although not significant, there were slightly lower Chl *a* concentrations in *Austrovenus* treatments relative to the controls for each sediment type. This is likely due to both the consumption of resuspended BMA (see *Chapter 4* and Shumway 1987, Sauriau and Kang 2000, Kang et al. 2006) and the burial of BMA by biodeposits and agrees with Thrush et al. (2006) who found an increase in microphyte standing stocks after the removal of *Austrovenus*. Thrush et al. (2006) also found no difference in the flux of oxygen under light and dark conditions in plots with and without *Austrovenus* but Sandwell et al. (2009) found a trend of increased GPP with increased *Austrovenus* density. Both Thrush et al. (2006) and Sandwell et al. (2009) found NH_4-N efflux to increase in areas with *Austrovenus*, or with increased densities of this species, which they attributed to the bulldozing of surface

sediments and interactions with microphytes. In my study, *Austrovenus* were not observed to move from their initial position within the cores over the study period (i.e., they did not behave normally and burrow into the sediments) which may account for the fact that no increase in NH_4-N flux was seen. Gross primary production in *Austrovenus* treatments did not differ between old and new sediments suggesting that the sedimentary environment is not an important factor in determining the role of this species on ecosystem functioning. This finding is, however, inconsistent with Jones et al. (2011) who found an increases in GPP in *Austrovenus* treatments in sandy sediments (relative to sandy sediment controls) but no change in GPP for *Austrovenus* treatments in muddy-sand sediments.

5.4.3. Disturbance, invertebrates and ecosystem functioning

The differences in primary production seen for the different invertebrate treatments in this study supports the notion that functional diversity plays an important role in ecosystem functioning (Emmerson et al. 2001, Waldbusser et al. 2004, Raffaelli 2006, Norling et al. 2007). Considering that benthic habitats and communities are exposed to a range of abiotic and biotic disturbances on varying spatial and temporal scales (Posey 1990) and that disturbances and their interactions are key factors in describing spatial and temporal patterns of diversity in estuarine ecosystems, it follows that disturbances may have a significant impact on the functioning of ecosystems. Interestingly, I was not able to conclude, as per Lohrer et al. (2010), that important ecological functions (primary production and nutrient efflux) were reduced in areas without large invertebrates. Rather, I found levels of GPP to be highest in treatments containing no large invertebrates (as well as *Austrovenus* treatments) as GPP was closely linked to Chl *a* concentration (under laboratory conditions) which was not reduced by consumption or burial in the control treatments. But, it must be appreciated that high productivity does not necessarily imply that the ecosystem is healthy and functioning optimally as BMA biomass is often highest in eutrophic areas (i.e., degraded habitats). Clearly, healthy ecosystems (i.e., those that are stable, sustainable and resilient to stress) are those which have high biodiversity and a range of functional species. Additionally, the comparison of single species treatments done in this study is not comparable to the majority of natural communities, where a large number of species and/or functional groups occur simultaneously. Consequently in estuaries, for example, there will often

be many species contributing to ecosystem functioning in different ways and the overall functioning will depend on the net effect of the entire community, which will depend on individual effects for each species. It is, however, important to examine the role of individual species within the system so that their role in the overall functioning of the ecosystem can be better understood. Differences between old and new sediments suggest that it is not only disturbance-driven impacts on community composition that can alter ecosystem functioning, but that the effects of disturbance on sedimentary characteristics are also important.

5.4.4. Summary

This chapter provides evidence that the introduction of large quantities of new sediments that covered 30-65% of the estuary surface after the February 2011 earthquake had a positive effect on the functioning of this ecosystem by increasing primary production and reducing nutrient efflux from areas of eutrophic sediments. By capping a large portion of eutrophic sediments, the release of legacy nutrients from the sediments to the overlying water was reduced at the two most eutrophic sites within the estuary. This supports my hypothesis that nutrient (especially NH_4-N) efflux would be greater in old sediments than in new sediments after the earthquake. More specifically, as old and new sediments mixed over time and developed and grew similar bacterial and microalgal communities, nutrient efflux became more similar between the two sediment types. Inconsistent with my hypothesis, GPP was found to be higher in new sediments than in old sediments at the eutrophic sites two months after the earthquake, despite higher BMA biomass and nutrient efflux in old sediments. This indicated that BMA in new sediments had increased photosynthetic efficiency which was probably driven by increased nutrient uptake by BMA in new sediments and greater permeability of new sediments enabling increased light penetration and enhanced solute flux. As expected, *Amphibola* reduced BMA biomass and consequently levels of GPP, and GPP for *Austrovenus* did not differ from the control in both old and new sediments. I also found *Austrohelice* to reduce levels of GPP, resulting from both the consumption and burial of BMA. In most cases, there was not a good correlation between nutrient availability and/or uptake and primary production despite my hypothesis that there would be a positive relationship between an increased nutrient efflux/uptake (particularly NH_4-N) and increased GPP. Overall, the results of this study indicate that functional diversity

and sedimentary characteristics can have important effects on primary production and nutrient flux and consequently the functioning of estuarine ecosystems. As such ecosystems are of high ecological and societal value, understanding relationships between habitats, diversity and ecosystem functioning is important, particularly in areas exposed to eutrophication and/or disturbances.

Chapter 6

Overall Summary and General Discussion

This thesis examined the response of estuarine invertebrates and their habitats to large-scale change. Specifically, this work focused on effects of reversal of eutrophication due to the offshore diversion of wastewater and cataclysmic earthquake events on Christchurch's Avon-Heathcote Estuary. Three key questions were addressed:

1) How do estuarine invertebrate communities and their habitats respond to large-scale change?

2) What are the impacts of large-scale change on estuarine invertebrate food webs?

3) How is ecosystem functioning, and the role of invertebrates in this process, affected by large-scale change?

To do this, I compared pre- and post-diversion and pre- and post-earthquake communities, sediment characteristics and isotopic values to examine the impacts of the wastewater diversion and earthquakes on the ecology of the estuary. Field- and laboratory-based experiments were used to test the effects of sediment type and invertebrate functional guilds on primary production and consequently ecosystem functioning in the context of eutrophication and disturbance. Here I present a detailed summary of the findings of my study and a general discussion of issues not covered in the discussions in individual chapters.

6.1. Consequences of eutrophication and earthquake-driven change on the structure and functioning of habitats and communities in the Avon-Heathcote Estuary: An expanded summary of results

I found considerable spatial heterogeneity in the structure of communities and their habitats which, prior to the earthquakes, was related to the eutrophication gradient that existed within the estuary. This gradient had been produced by the proximity of sites to the former discharge pipe, combined with the varying tidal flows and other hydrodynamic features of the estuary. Tidal flows on the western side of the estuary were generally low and sites in this backwater, low-circulation area were the most eutrophic. These sites had relatively cohesive sediments with high levels of organic

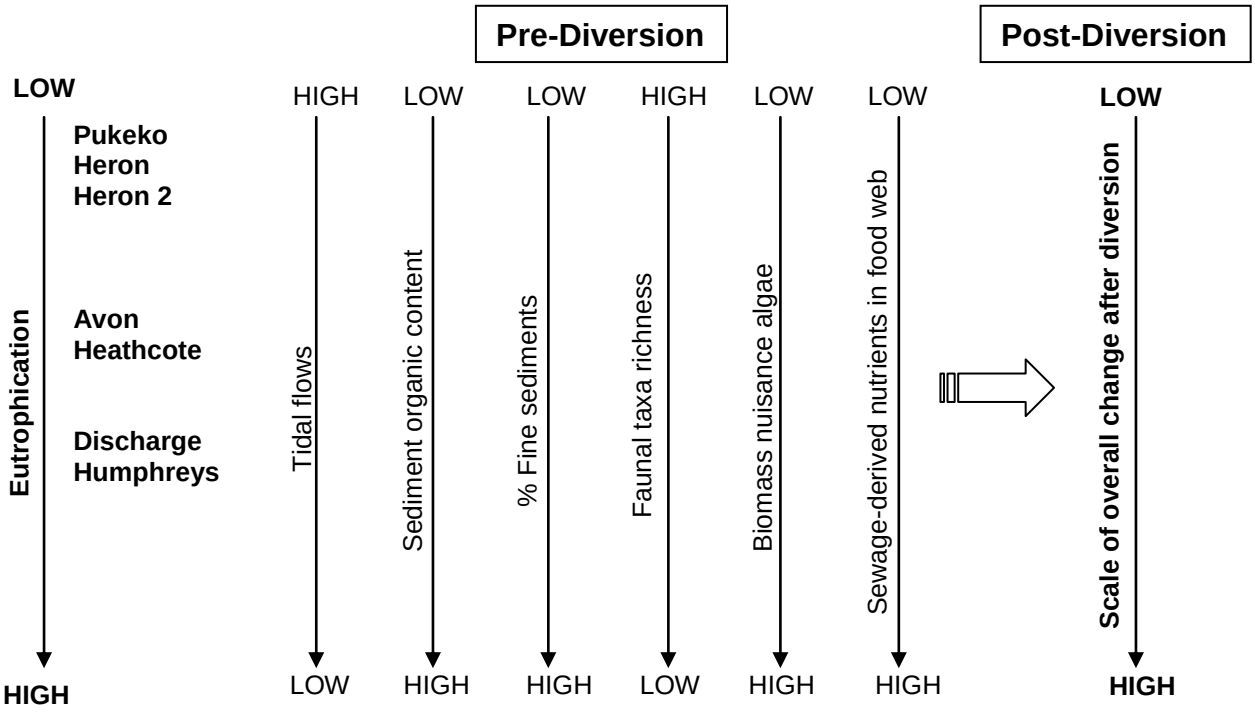

Figure 6.1. Synthesis of the tidal, sediment and community gradients occurring across the site eutrophication gradient and trajectories of recovery. Note that the prevalence of sewage-derived nutrients in the food web were not examined at Heron 2 and Humphreys (but are likely to be low and high respectively)

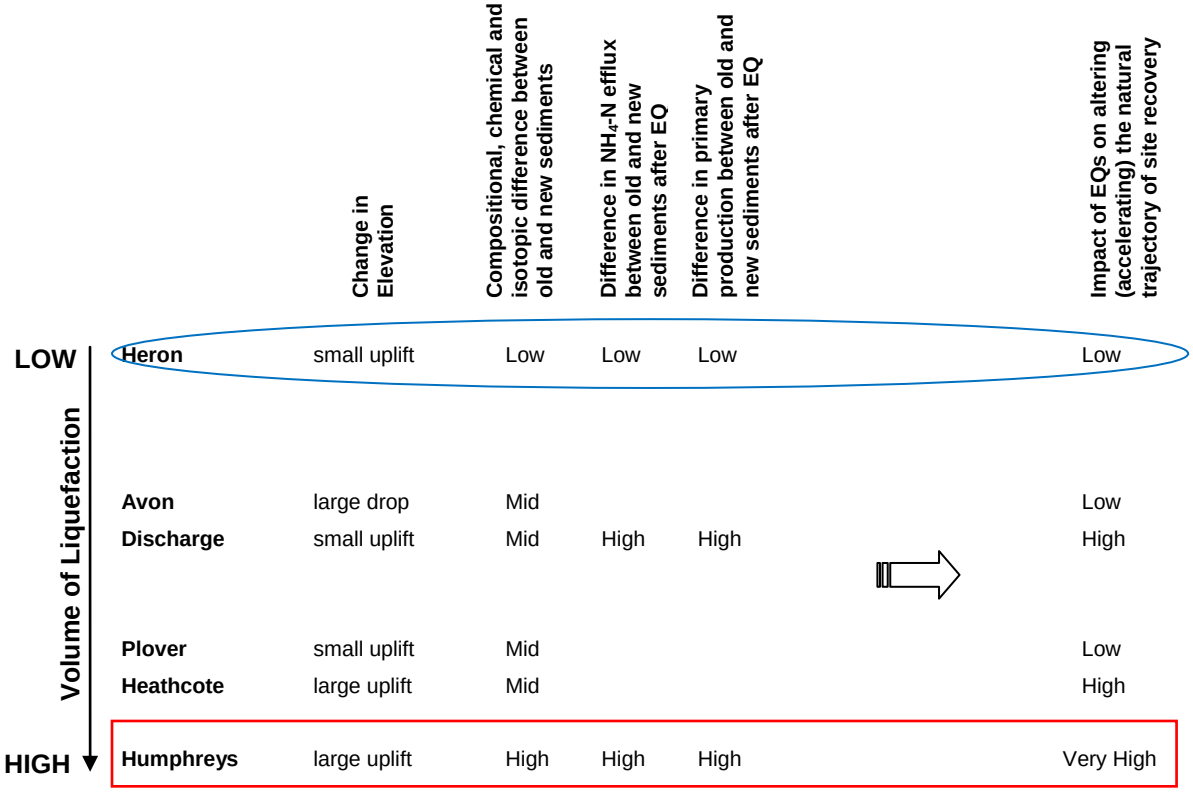

Figure 6.2. Synthesis of the general relative impacts of the earthquakes at the six sites studied. Sites are arranged in a gradient reflecting the amount of liquefaction they received. Heron, the least eutrophic site (which received a low amount of liquefaction), is circled in blue and Humphreys, the most eutrophic site (which received a high amount of liquefaction), is shown in the red rectangle.

matter, a higher biomass of nuisance algae, reduced faunal taxa richness with a higher proportion of opportunistic species, and a high amount of sewage-derived nutrients being used by benthic microalgae (BMA) and subsequently becoming incorporated into the food web (Fig. 6.1). After the wastewater diversion offshore, the proportional changes that occurred at each site were strongly related to its pre-diversion eutrophication status. Generally, the eutrophic sites showed the greatest amount of change with regards to habitat, community and food web characteristics whereas the “clean” sites, on the eastern side of the estuary, did not change greatly.

Clearly, the earthquakes altered the “natural” trajectory of community and sediment recovery after the diversion. The impact of the earthquakes on estuarine habitats, communities and their effect in altering the natural trajectory of recovery depended on two key factors: the amount of liquefaction occurring at each site and the eutrophication status of individual sites. Also important were the changes in bed height after the 22 February 2011 earthquake (altering the area of sediment exposed at low tide) and the amount of raw sewage being received by sites (Fig. 6.2). Spatially, the composition of new sediments was fairly uniform across the estuary. The new sediments were coarser, had lower amounts of organic matter, were much less polluted and were largely devoid of fauna. The relative differences between old and new sediments, however, varied among sites. At the eutrophic sites, old and new sediments were vastly different but at the cleaner sites they were more similar. New sediments were less eutrophic than the surrounding old sediments, releasing much less NH_4-N than the old sediments at the eutrophic sites after the February 2011 earthquake. Thus the input of large quantities of new sediments has in one sense accelerated the recovery of the estuary by burying and capping a large portion of the eutrophic sediments particularly at Discharge and Humphreys (Fig. 6.2). Even as the new sediments dispersed and mixed with old sediments, the capping effect remained and became stronger because the mixing of old and new sediments reduced the amount of NH_4-N released from areas of previously uncapped old sediments.

Benthic microalgae (BMA) played significant roles in multiple aspects of this study. Trophically, BMA were important in supporting consumers and were the dominant food source for the mud snail *Amphibola crenata*. Surprisingly, they were also a key food source (when resuspended) for the filter-feeding cockle *Austrovenus stutchburyi*. Unlike *Ulva lactuca* and *Gracilaria chilensis*, the tissues of which

reflected the nitrogen sources present in the water column, BMA were found to rely largely on the uptake of sediment-derived nutrients that they intercepted at the sediment-water interface. This sewage-derived nitrogen was subsequently reflected in the isotopic values of the invertebrate consumers at the eutrophic sites as it became incorporated into the food web. Benthic microalgae were also found to play a crucial role in influencing levels of primary production (in combination with other factors like light intensity and nutrient flux). At high biomasses, primary production was reduced (i.e., peaks were in the mid-biomass range), probably because individual BMA became shaded and there was increased competition for light and nutrients. Consequently, it is important to understand that although BMA are important components of estuarine ecosystems, their high biomass, generally found in eutrophic areas can have adverse effects on ecosystem functioning and is often indicative of a nutrient-rich habitat.

Invertebrate communities were clearly affected by eutrophication and the earthquakes. Some impacts were direct, such as burial by liquefaction (seen in long cores) and probable mortality from nitrogen loading (although this was not delineated in this study), resulting in reduced taxa richness and an increased abundance of opportunistic species. Through time, changes in faunal community composition occurred due to the reduction in nitrogen input (from the diversion) and the mixing of old and new sediments after the earthquake. Indirectly, invertebrates were affected by changes to their food sources, and shifts in the isotopic values of primary producers (due to the reduced uptake of sewage-derived nutrients) were reflected in invertebrate tissues. Changes were, however, site-specific with the isotopic values of consumers (e.g., *Amphibola* and *Austrovenus*) at the eutrophic Discharge site changing the most over time to become more similar to consumers at the less eutrophic sites. Isotopic values of consumers at the two river sites were similar and were more enriched than values at Discharge but more depleted than those at the "clean" sites (Heron and Pukeko) where there was little temporal change. Interestingly, although primary producer assemblages in the estuary changed in response to the diversion and earthquakes, for example the disappearance of *Gracilaria* and *Ulva* at Humphreys and the subsequent dominance of BMA at this site, the primary producers supporting estuarine consumers seemed to be independent of their relative biomass. That is, the diet of specific consumer species (e.g., *Amphibola*, *Austrovenus* and crab species) across spatial and temporal scales

was similar (despite spatial/temporal differences in the biomass of primary producers) and variations in isotopic signatures were due to changes in the source of dissolved nutrients being used by primary producers, not changes in diet. Although the input of raw sewage after the earthquakes was reflected in the tissues of macroalgae, the earthquakes did not appear to affect the isotopic composition of consumers, indicating that the relatively short nature of the inputs was too brief to become incorporated into the estuarine food web.

Not only were habitat characteristics found to be important in structuring invertebrate communities but experimental work showed the importance of invertebrate functional traits in modifying habitats. For example, primary production can be used as an indicator of ecosystem functioning and it varied in different invertebrate treatments. *Amphibola* was found to graze on BMA and reduce productivity whereas the effect of *Austrovenus* of primary production was minimal although these cockles did not appear to behave "normally" throughout the experiment (they did not burrow as expected). Production in *Austrohelice* treatments was relatively low, and influenced by the consumption and burial of BMA. Because functional diversity was found to be an important driver of primary production it can be extrapolated that in instances when functional diversity is low (e.g., after the earthquakes or in eutrophic areas), the functioning of the ecosystem is altered and will reflect the functional traits of those species that can persist in these conditions.

Overall, the large quantities of new sediments introduced into the estuary by the earthquakes have had a positive effect on its recovery by capping large areas of eutrophic sediments and providing better habitat for estuarine communities. It is important to acknowledge that although the sites chosen in this study represented the broad range of habitats present within the Avon-Heathcote Estuary, and thereby covered eutrophic and earthquake disturbance gradients, within-site sampling was spatially limited because of logistic restraints. Sites in the mid-upper shore were considered the most important as these were areas where the eutrophication and disturbance gradients were best represented and where the trajectory of habitat change and recovery could be best examined. In these areas, they have all improved.

6.2. Spatial and temporal scales in the recovery of the Avon-Heathcote Estuary following eutrophication and earthquake events: What constitutes a recovery?

During the 10 months between the wastewater-diversion and the February 2011 earthquake there were signs that recovery was beginning within the Avon-Heathcote Estuary. For example, the $\delta^{13}C$ values of *Amphibola* at Discharge were becoming more similar to values of these invertebrates at the cleaner sites and the biomass of nuisance macroalgae was decreasing. It is interesting to consider, however, what constitutes a recovery: what ecological end point is considered a successful recovery for the Avon-Heathcote Estuary, or other recovering ecosystems? Consistent with Elliott et al. (2007), the term “recovery” implies that an area is currently in a more degraded condition and will return to a previous condition of increased ecological health, where the community will have similar species composition, population density, size and biomass to that present in the historical baseline ecosystem. However, in many instances, such historical conditions are not known and it can be difficult to determine what the natural and pristine conditions were. Furthermore, it has been questioned whether baseline conditions can actually be achieved, even in cases where they are known, with some systems recovering to an improved, but alternative, state (Simenstad et al. 2006). Such ‘hysteresis’ can occur when the trajectory of change to the system following the removal of the stress (e.g., excess nutrients) differs from the trajectory that was followed as the stress was applied (e.g., during increased eutrophication (Beisner et al. 2003, Webster and Harris 2004)). Sometimes, recovery to the conditions present at a comparable unimpacted site may be used or a desired set of characteristics for a particular ecosystem established that efforts can be targeted towards (Zajac and Whitlatch 2001). For the Avon-Heathcote Estuary, historical ecological conditions are not well known and recovery to near pristine conditions is highly unlikely given its urban location, long history of wastewater input, and other human impacts such as armouring, the nearby oxidation ponds and altered wetlands. Consequently, in this case, a suitable recovery target may be to aim for a desired set of ecosystem characteristics, such as:

- increased diversity and a reduction in opportunistic N-utilising species;
- disappearance of nuisance algae (and, in turn, removing the “bad smell” caused by this rotting algae);

- spread of seagrass to more sites and across a greater tidal range; current seagrass beds to become more dense;
- improved sediment health through diminished organic content and a deeper oxic layer;
- re-establishment of recreational shellfish collection and fishing;
- more attractive conditions for increased recreational usage, such as swimming, windsurfing, kiteboarding and picnicing

The time frame of recovery is also important and that of my study (2.5 years) was much shorter than the average recovery times reported for other aquatic ecosystems. For example, Jones and Schmitz (2009) found that the average recovery times for both brackish and marine systems was 10-20 years and Borja et al. (2010) reported that full recovery of these systems can take a minimum of 15-25 years. I found evidence of some recovery at the most eutrophic sites, such as the disappearance of algae at Humphreys and improved sediment condition due to the introduction of new sediments from the earthquakes. However, there was little evidence of increased taxa richness of the faunal communities in these heavily eutrophied sites and there was still a preponderance of old organic-rich sediments. The different ecosystem components are recovering at different rates and there is still much recovery to go in some areas of the estuary.

My study appears unique in that pre-diversion and pre-earthquake data were collected. Most studies (approximately 80% according to Jones and Schmitz (2009)) only have post-disturbance/restoration effort data available, which makes it much more difficult to determine the impacts of the disturbance and/or to determine the success of restoration measures. I can find no example of a study that occurred intensively before and after a highly disruptive earthquake.

Spatially, recovery will proceed at different rates at different sites and this will depend on several factors. Clearly, the scale, intensity and duration of the stress/disturbance are initially important but beyond this, it is the physical and biological features of the site such as water flows, wave action/currents which influence the amount of flushing and the introduction of new propagules/larvae, the species involved, bioturbation activity, denitrification and the continued mixing of sediments, which will influence rates of recovery. As discussed previously, the

gradient of eutrophication within the estuary means that the amount of recovery required at some sites (the most eutrophic sites) to reach a determined “optimal endpoint” is much greater than that required at others (the “clean” sites). This is due to several factors including the large amounts of legacy nitrogen that are stored in the sediments at the eutrophic sites, low amounts of bioturbation and the fact that these sites are in a tidal-backwash area of the estuary where there is less flushing and probably a reduced abundance of colonising propagules/larvae. In addition to this, the uplifting of the estuary floor and upheaval of large amounts of sediments at these eutrophic sites, particularly Humphreys, has been positive in several ways (e.g., by introducing large amounts of clean and coarse low nutrient sediments and capping large portions of eutrophic sediments) but it has also worsened the already poor circulation at these sites and increased the exposure time of sediments. Lastly, one negative sociological aspect of the uplifting of the eastern side of the estuary is that it has made this area too shallow for kite boarders.

6.3. Management Implications

Estuaries worldwide are declining in environmental quality due to the increased eutrophication of these often urban-located water bodies from human alterations to the natural environment (Lillebo et al. 2005). The management of these areas has thus become increasingly important. Ideally, management should focus on protection measures to prevent further degradation, but the implementation of such measures is often difficult and they have, at best, been applied to only a small portion of natural systems (Valiela et al. 2000). Due to the continued exploitation and alteration of ecosystems by anthropogenic activities, however, most often it is the restoration of eutrophied areas that becomes the focus. Following the removal of the stress (e.g., nutrient loading), estuarine ecosystems can either be left to recover naturally, or their recovery can be mediated through intervention measures**.** For example, it has been suggested that interventions such as dredging can reduce the internal nutrient load of some eutrophic systems through the biostimulatory release of nutrients (Wattayakorn 2002). There have, however, been very few studies of this and most of them have been done on smaller, experimental scales (Lohrer and Wetz 2003, Zhang et al. 2010). The ‘capping’ of eutrophic sediments is another remediation technique for contaminated sediments, which can prevent or reduce the release of internal nutrients and/or pollutants to the water column via advection, diffusion, re-

suspension and/or bioturbation (Wang et al. 1991, Zeman 1994, Azcue et al. 1998, Welch 1999, Huang et al. 2011). Unlike my study, where the capping of eutrophic sediments occurred via natural processes, capping is usually a planned intervention measure often occurring in lakes. Here, eutrophic sediments are sealed off from the water column by placing a cover over the sediments. This cover can be composed of natural materials like sand, gravel and clay that act as a passive physical barrier, or non-natural materials like zeolite, ceramicite and light porous media which act as active barriers and react with and remove nutrients/contaminants (Wang et al. 1991, Zeman 1994, Jacobs and Forstner 1999, Huang et al. 2011). In some cases, 90-100% of total nitrogen in the overlying water has been removed by capping sediments (Huang et al. 2011). The effectiveness of capping through time depends on the amount of erosion to the capping material and its displacement by tides and currents. Furthermore, in most aquatic systems the capping layer will become buried over time through the input of sediments and organic matter from the catchment. The burial rate will depend on the sedimentation rates and the rates of input and settlement of organic matter but once deposited, the decomposition of organic matter will fuel the release of nutrients from the sediments (Welch 1999). Consequently capping generally works best in the short to medium term or in combination with other concurrent catchment remediation measures (Hickey and Gibbs 2009).

As discussed in the previous section, the concept of a recovery is fluid and must take into account the priorities of different stakeholders and user groups, the funds available for the project and any pressures to achieve results (improvements) in a timely fashion. Sometimes, this may require managers to consider difficult questions such as “what components of the ecosystem should we be most concerned about,” and, “are there useless species and dispensable processes” that can be deprioritised (Valiela et al. 2000). Clearly, the answers to such questions will be subjective and may differ considerably among different stakeholders. The success of ecosystem-based management then becomes an issue of setting and achieving the best set of outcomes for all parties involved. To achieve this, a holistic approach that considers habitats, communities and processes over a wide range of spatial and temporal scales and that incorporates research carried out over all levels of ecological organisation (Christensen et al. 1996) is required.

6.4. Conclusion

In the case of the Avon-Heathcote Estuary, the $89 million investment in wastewater diversion seems to be money well spent. Nutrient abatement in the water column was undoubtedly a necessary precursor of positive change. However, it was not sufficient, at least in the short term, to affect a considerable amount of change. This required the upheaval of new sediments which, by and large, brought increased sediment health. Despite continuing issues relating to sediment loading of the two rivers, altered flows and elevation changes, the “ecosystem” indicators of the Avon-Heathcote Estuary have all improved through a combination of human-induced and natural remediation.

The diversion and earthquake events have enabled me to test the potentially synergistic effects of nutrient reduction and earthquake disturbance on invertebrate communities, associated habitats and food web dynamics. Although the trajectory of recovery after the diversion has been confounded due to the earthquakes, it is hoped that the two-and-a-half year data set collected as part of my PhD, alongside data that will continue to be collected as part of the wider Avon-Heathcote Estuary project, will be of considerable use to environmental managers, councils and governmental departments who may be contemplating other large diversion procedures in the future. Understanding the fundamental ecological processes that occur following wastewater diversions of this scale are vital for underpinning management decisions that will assess the benefits of nitrogen reduction on the many impacted estuaries in New Zealand and worldwide.

Finally, to the best of my knowledge, there are no other published studies examining the impacts of large earthquakes on benthic communities in an estuarine ecosystem. The series of earthquakes that occurred in Canterbury New Zealand have provided me with a novel opportunity to investigate the impact of these natural disturbance events on estuarine communities. I hope that this research will contribute to an increased scientific understanding of the ecological processes that occur following a natural disturbance event of this scale.

References

Adams, N. M. 1994. Seaweeds of New Zealand: An illustrated guide. Canterbury University Press, Christchurch.

Agard, J. B. R., J. Gobin, and R. M. Warwick. 1993. Analysis of marine macrobenthic community structure in relation to pollution, natural oil seepage and seasonal disturbance in a tropical environment (Trinidad, West-Indies). Marine Ecology Progress Series **92**:233-243.

Allan, E. L., S. T. Ambrose, N. B. Richoux, and P. W. Froneman. 2010. Determining spatial changes in the diet of nearshore suspension-feeders along the South African coastline: Stable isotope and fatty acid signatures. Estuarine Coastal and Shelf Science **87**:463-471.

Aller, R. C. 2001. Transport and reactions in the bioirrigated zone. Oxford University Press, Oxford.

Alvarez-Filip, L., M. Millet-Encalada, and H. Reyes-Bonilla. 2009. Impact of Hurricanes Emily and Wilma on the coral community of Cozumel Island, Mexico. Bulletin of Marine Science **84**:295-306.

Andersen, F. O. and E. Kristensen. 1988. The influence of macrofauna on estuarine benthic community metabolism - A microcosm study. Marine Biology **99**:591-603.

Apodaca, J. J., J. C. Trexler, N. K. Jue, M. Schrader, and J. Travis. 2013. Large-scale natural disturbance alters genetic population structure of the sailfin molly, *Poecilia latipinna*. American Naturalist **181**:254-263.

Armitage, A. R. and J. W. Fourqurean. 2009. Stable isotopes reveal complex changes in trophic relationships following nutrient addition in a coastal marine ecosystem. Estuaries and Coasts **32**:1152-1164.

Askins, R. A. and D. N. Ewert. 1991. Impact of Hurricane Hugo on bird populations on St-John, United-States Virgin-Islands. Biotropica **23**:481-487.

Asmus, H. and R. Asmus. 1985. The importance of grazing food-chain for energy-flow and production in 3 intertidal sand bottom communities of the Northern Wadden Sea. Helgolander Meeresuntersuchungen **39**:273-301.

Attiwill, P. M. 1994. The disturbance of forest ecosystems - the ecological basis for conservative management. Forest Ecology and Management **63**:247-300.

Azcue, J. M., A. J. Zeman, A. Mudroch, F. Rosa, and T. Patterson. 1998. Assessment of sediment and porewater after one year of subaqueous capping of contaminated sediments in Hamilton Harbour, Canada. Water Science and Technology **37**:323-329.

Baeta, A., R. Pinto, I. Valiela, P. Richard, N. Niquil, and J. C. Marques. 2009a. Delta N-15 and delta C-13 in the Mondego estuary food web: Seasonal variation in producers and consumers. Marine Environmental Research **67**:109-116.

Baeta, A., I. Valiela, F. Rossi, R. Pinto, P. Richard, N. Niquil, and J. C. Marques. 2009b. Eutrophication and trophic structure in response to the presence of the eelgrass *Zostera noltii*. Marine Biology **156**:2107-2120.

Bahlburg, H. and R. Weiss. 2007. Sedimentology of the December 26, 2004, Sumatra tsunami deposits in eastern India (Tamil Nadu) and Kenya. International Journal of Earth Sciences **96**:1195-1209.

Baker, W. L. 1990. Species richness of Colorado riparian vegetation. Journal of Vegetation Science **1**:119-124.

Barnes, R. S. K. 1984. Estuarine Biology. Second Edition edition. Edward Arnold (Publishers) Ltd., London.

Barr, N. 2007. Aspects of nitrogen metabolism in the green alga *Ulva*; Developing an indicator of seawater nitrogen loading. University of Auckland.

Barr, N., Zeldis, J., Gongol, D., Drummond, L., Scheuer, K. 2012. Effects of the Canterbury earthquakes on Avon-Heathcote Estuary/Ihutai macroalgae. Report prepared for Environment Canterbury and Christchurch City Council.

Barr, N. G., B. D. Dudley, K. M. Rogers, and C. D. Cornelisen. 2013. Broad-scale patterns of tissue-delta15N and tissue-N indices in frondose *Ulva* spp.; developing a national baseline indicator of nitrogen-loading for coastal New Zealand. Marine Pollution Bulletin **67**:203-216.

Beardall, J., S. Beer, and J. A. Raven. 1998. Biodiversity of marine plants in an era of climate change: Some predictions based on physiological performance. Botanica Marina **41**:113-123.

Bearlin, A. R., M. A. Burgman, and H. M. Regan. 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Phillip Bay, Victoria, Australia. Ecological Modelling **118**:131-148.

Beer, C. G. 1959. Notes of the behaviour of two estuarine crab species. Transactions of the Royal Society of New Zealand **86**:197-203.

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment **1**:376-382.

Bemvenuti, C. E. 1987. Predation effects on a benthic community in estuarine soft sediments. Atlantica **9**:5-32.

Benedetti-Cecchi, L., F. Pannacciulli, F. Bulleri, P. S. Moschella, L. Airoldi, G. Relini, and F. Cinelli. 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. Marine Ecology Progress Series **214**:137-150.

Berkes, F., Colding, J., Folke, C. 2003. Navigating social-ecological systems: Building resilience for complexity and change Cambridge University Press, Cambridge, UK.

Biles, C. L., D. M. Paterson, R. B. Ford, M. Solan, and D. G. Raffaelli. 2002. Bioturbation, ecosystem functioning and community structure. Hydrology and Earth System Sciences **6**:999-1005.

Bird, C. J., W. A. Nelson, E. L. Rice, K. G. Ryan, and R. Villemur. 1990. A critical comparison of *Gracilaria-chilensis* and *G-sordida* (Rhodophyta, Gracilariales). Journal of Applied Phycology **2**:375-382.

Bjornsater, B. R. and P. A. Wheeler. 1990. Effect of nitrogen and phosphorus supply on growth and tissue composition of *Ulva fenestrata* and *Enteromorpha intestinalis* (Ulvales, Chlorophyta). Journal of Phycology **26**:603-611.

Blomster, J., C. A. Maggs, and M. J. Stanhope. 1998. Molecular and morphological analysis of *Enteromorpha intestinalis* and *E-compressa* (Chlorophyta) in the British Isles. Journal of Phycology **34**:319-340.

Bode, A., M. T. Alvarez-Ossorio, and M. Varela. 2006. Phytoplankton and macrophyte contributions to littoral food webs in the Galician upwelling estimated from stable isotopes. Marine Ecology Progress Series **318**:89-102.

Bolam, S. G., T. F. Fernandes, and M. Huxham. 2002. Diversity, biomass, and ecosystem processes in the marine benthos. Ecological Monographs **72**:599-615.

Bolam, S. G., Fernandes, T.F., Read, P., Raffaelli, D. 2000. Effects of macroalgal mats on intertidal sandflats: An experimental study. Journal of Experimental Marine Biology and Ecology **249**:123-137.

Bolton-Richie, L. 2008. Water quality of the Avon-Heathcote Estuary/Ihutai. Environment Canterbury. Christchurch, New Zealand.

Bolton-Richie, L. 2011. The sediments and biota of the Avon-Heathcote Estuary/Ihutai and the tidal reaches of the Avon and Heathcote rivers. Environment Canterbury, Christchurch, New Zealand

Bolton-Richie, L., Main, M. 2005. Nutrient water quality in the Avon-Heathcote Estuary/Ihutai. Inputs, concentrations and potential effects. Enivronment Canterbury, Christchurch, New Zealand

Bolton-Ritchie, L. 2012. Water quality of the Avon-Heathcote Estuary/Ihutai. Environment Canterbury, Christchurch, New Zealand.

Borja, A., D. M. Dauer, M. Elliott, and C. A. Simenstad. 2010. Medium- and long-term recovery of estuarine and coastal ecosystems: Patterns, rates and restoration effectiveness. Estuaries and Coasts **33**:1249-1260.

Bostrom, C. and E. Bonsdorff. 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L) beds in the northern Baltic Sea. Journal of Sea Research **37**:153-166.

Bostrom, C. and E. Bonsdorff. 2000. Zoobenthic community establishment and habitat complexity - the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. Marine Ecology Progress Series **205**:123-138.

Bostrom, C., E. Bonsdorff, P. Kangas, and A. Norkko. 2002. Long-term changes of a brackish-water eelgrass (*Zostera marina* L.) community indicate effects of coastal eutrophication. Estuarine Coastal and Shelf Science **55**:795-804.

Botto, F. and O. Iribarne. 2000. Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. Estuarine Coastal and Shelf Science **51**:141-151.

Bridges, T. S., Berry, W.J., Della, S.S., Dorn, P.B., Ells, S.J., Gries, T.H., Ireland, D.S., Maher, E.M., Menzie, C.A., Porebski, L.M., Stronkhorst, J. 2005. A framework for assessing and managing risks from contaminated sediments.*in* R. J. Wenning, Batley, G.E., Ingersoll, C.G., Moore, D.W., editor. Use of sediment quality guidelines (SQGs) and related tools for the assessment of contaminated sediments. Pensacola (FL): Society of Environmental Toxicology and Chemistry.

Brooks, R. A. and S. S. Bell. 2001. Mobile corridors in marine landscapes: Enhancement of faunal exchange at seagrass/sand ecotones. Journal of Experimental Marine Biology and Ecology **264**:67-84.

Brotas, V., Cabrita, T., Portugal, A., Serodio, J., Catarino, F. . 1995. Spatiotemporal distribution of the microphytobenthic biomass in intertidal flats of Tagus Estuary (Portugal). Hydrobiologia **300**.

Buffan-Dubau, E. and K. R. Carman. 2000. Extraction of benthic microalgal pigments for HPLC analyses. Marine Ecology Progress Series **204**:293-297.

Bulling, M. T., P. C. L. White, D. G. Raffaelli, and G. J. Pierce. 2006. Using model systems to address the biodiversity-ecosystem functioning process. Marine Ecology Progress Series **311**:295-309.

Cahoon, L. B., J. E. Nearhoof, and C. L. Tilton. 1999. Sediment grain size effect on benthic microalgal biomass in shallow aquatic ecosystems. Estuaries **22**:735-741.

Cahoon, L. B., Safi, K.A. 2002. Distribution and biomass of benthic microalgae in Manukau Harbour, New Zealand. New Zealand Journal of Marine and Freshwater Research **4**.

Candia, A., M. A. Gonzalez, R. Montoya, P. Gomez, and W. Nelson. 1999. Comparison of ITS RFLP patterns of Gracilaria (Rhodophyceae, Gracilariales) populations from Chile and New Zealand and an examination of interfertility of Chilean morphotypes. Journal of Applied Phycology **11**:185-193.

Canuel, E. A., A. C. Spivak, E. J. Waterson, and J. E. Duffy. 2007. Biodiversity and food web structure influence short-term accumulation of sediment organic matter in an experimental seagrass system. Limnology and Oceanography **52**:590-602.

Castilla, J. C. 1988. Earthquake-caused coastal uplift and its effects on rocky intertidal kelp communities. Science **242**:440-443.

Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science **277**:500-504.

Chaves, J. 2004. Potential use of d15N to assess nitrogen sources and fate in Narragansett Bay. PhD Thesis. .

Cheung, S. G., N. W. Y. Lam, R. S. S. Wu, and P. K. S. Shin. 2008. Spatio-temporal changes of marine macrobenthic community in sub-tropical waters upon recovery from eutrophication. II. Life-history traits and feeding guilds of polychaete community. Marine Pollution Bulletin **56**:297-307.

Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. Dantonio, R. Francis, J. F. Franklin, J. A. MacMahon, R. F. Noss, D. J. Parsons, C. H. Peterson, M. G. Turner, and R. G. Woodmansee. 1996. The report of the ecological society of America committee on the scientific basis for ecosystem management. Ecological Applications **6**:665-691.

Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. Marine Ecology Progress Series **210**:223-253.

Cole, M. L., K. D. Kroeger, J. W. McClelland, and I. Valiela. 2006. Effects of watershed land use on nitrogen concentrations and delta(15) nitrogen in groundwater. Biogeochemistry **77**:199-215.

Cole, M. L., I. Valiela, K. D. Kroeger, G. L. Tomasky, J. Cebrian, C. Wigand, R. A. McKinney, S. P. Grady, and M. H. C. da Silva. 2004. Assessment of a delta ^{15}N isotopic method to indicate anthropogenic eutrophication in aquatic ecosystems. Journal of Environmental Quality **33**:124-132.

Colijn, F. and K. S. Dijkema. 1981. Species composition of benthic diatoms and distribution of Chlorophyll-a on an inter-tidal flat in the Dutch Wadden Sea. Marine Ecology Progress Series **4**:9-21.

Connell, J. H. 1987. Diversity in tropical rain-forests and coral reefs. Current Contents/Agriculture Biology & Environmental Sciences:16-16.

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist **111**:1119-1144.

Cook, P. L. M., D. Van Oevelen, K. Soetaert, and J. J. Middelburg. 2009. Carbon and nitrogen cycling on intertidal mudflats of a temperate Australian estuary. IV. Inverse model analysis and synthesis. Marine Ecology Progress Series **394**:35-48.

Cornelisen, C. D., S. R. Wing, K. L. Clark, M. H. Bowman, R. D. Frew, and C. L. Hurd. 2007. Patterns in the delta ^{13}C and delta ^{15}N signature of *Ulva pertusa*:

Interaction between physical gradients and nutrient source pools. Limnology and Oceanography **52**:820-832.

Dan, A., M. Hiraoka, M. Ohno, and A. T. Critchley. 2002. Observations on the effect of salinity and photon fluence rate on the induction of sporulation and rhizoid formation in the green alga *Enteromorpha prolifera* (Muller) J. Agardh (Chlorophyta, Ulvales). Fisheries Science **68**:1182-1188.

Davis, M. W. and C. D. McIntire. 1983. Effects of physical gradients on the production dynamics of sediment-associated algae. Marine Ecology Progress Series **13**:103-114.

Day, J. H. 1980. What is an estuary. South African Journal of Science **76**:198-198.

Day, J. H. 1981. Estuarine Ecology: With particular reference to southern Africa. Balkema, A.A., Rotterdam.

Deegan, L. A. and R. H. Garritt. 1997. Evidence for spatial variability in estuarine food webs. Marine Ecology Progress Series **147**:31-47.

DeNiro, M., Epstein, S. . 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta **42**:495-506.

Dennison, W. C., R. J. Orth, K. A. Moore, J. C. Stevenson, V. Carter, S. Kollar, P. W. Bergstrom, and R. A. Batiuk. 1993. Assessing water-quality with submersed aquatic vegetation. BioScience **43**:86-94.

Dernie, K. M., M. J. Kaiser, and R. M. Warwick. 2003. Recovery rates of benthic communities following physical disturbance. Journal of Animal Ecology **72**:1043-1056.

Diaz-Jaramillo, M., R. Socowsky, L. M. Pardo, J. M. Monserrat, and R. Barra. 2013. Biochemical responses and physiological status in the crab *Hemigrapsus crenulatus* (Crustacea, Varunidae) from high anthropogenically-impacted estuary (Lenga, south-central Chile). Marine Environmental Research **83**:73-81.

Diaz, R. J. and R. Rosenberg. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. Pages 245-303 *in* A. D. Ansell, R. N. Gibson, and M. Barnes, editors. Oceanography and Marine Biology - an Annual Review, Vol 33.

Diaz, R. J. and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. Science **321**:926-929.

Dittmann, S. 2000. Zonation of benthic communities in a tropical tidal flat of north-east Australia. Journal of Sea Research **43**:33-51.

Dobbinson, S. J., Barker, M.F., Jillett, J.B. 1989. Experimental shore level transplantation of the New Zealand cockle *Chione stutchburyi*. Journal of Shellfish Research **8**:197-212.

Duarte, C. M. 1999. Seagrass ecology at the turn of the millennium: Challenges for the new century. Aquatic Botany **65**:7-20.

Duncan, R. P. 1993. Flood disturbance and the coexistence of species in a lowland podocarp forest, South Westland, New Zealand. Journal of Ecology **81**:403-416.

Dyer, K., R,. 1979. Estuarine hydrography and sedimentation: A handbook. Cambridge University Press, Cambridge.

Edgar, G. J. and A. I. Robertson. 1992. The influence of seagrass structure on the distribution and abundance of mobile epifauna - pattern and process in a Western-Australian *Amphibolis* bed. Journal of Experimental Marine Biology and Ecology **160**:13-31.

Edgar, G. J. and C. Shaw. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia .1. Species richness, size-structure and production of fishes in Western Port, Victoria. Journal of Experimental Marine Biology and Ecology **194**:53-81.

Eggeling, W. J. 1947. Observations on the ecology of the Budongo Rain Forest, Uganda. Journal of Ecology **34**:20-&.

Elliott, M., D. Burdon, K. L. Hemingway, and S. E. Apitz. 2007. Estuarine, coastal and marine ecosystem restoration: Confusing management and science - A revision of concepts. Estuarine Coastal and Shelf Science **74**:349-366.

Elliott, M. and V. Quintino. 2007. The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Marine Pollution Bulletin **54**:640-645.

Emmerson, M. C., M. Solan, C. Emes, D. M. Paterson, and D. Raffaelli. 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. Nature **411**:73-77.

Engle, V. D., J. L. Hyland, and C. Cooksey. 2009. Effects of Hurricane Katrina on benthic macroinvertebrate communities along the northern Gulf of Mexico coast. Environmental Monitoring and Assessment **150**:193-209.

Escapa, M., G. M. E. Perillo, and O. Iribarne. 2008. Sediment dynamics modulated by burrowing crab activities in contrasting SW Atlantic intertidal habitats. Estuarine Coastal and Shelf Science **80**:365-373.

Essink, K. 2003. Response of an estuarine ecosystem to reduced organic waste discharge. Aquatic Ecology **37**:65-76.

Estes, J. A. and J. F. Palmisan. 1974. Sea otters - their role in structuring nearshore communities. Science **185**:1058-1060.

Falkowski, P. and D. A. Kiefer. 1985. Chlorophyll-a fluorescence in phytoplankton - relationship to photosynthesis and biomass. Journal of Plankton Research **7**:715-731.

Fang, L. S., I. S. Chen, K. S. Tew, C. C. Han, T. F. Lee, and I. M. Chen. 2002. Impact of the 1999 earthquake on mountain stream fishes in Taiwan. Fisheries Science **68**:446-448.

Ferrell, D. J. and J. D. Bell. 1991. Differences among assemblages of fish associated with *Zostera-capricorni* and bare sand over a large spatial scale. Marine Ecology Progress Series **72**:15-24.

Fertig, B., T. J. B. Carruthers, W. C. Dennison, A. B. Jones, F. Pantus, and B. Longstaff. 2009. Oyster and macroalgae bioindicators detect elevated delta N-15 in Maryland's coastal bays. Estuaries and Coasts **32**:773-786.

Fielding, P. J., K. S. J. Damstra, and G. M. Branch. 1988. Benthic diatom biomass, production and sediment Chlorophyll in langebaan lagoon, South-Africa. Estuarine Coastal and Shelf Science **27**:413-426.

Ford, R. B. and C. Honeywill. 2002. Grazing on intertidal microphytobenthos by macrofauna: Is pheophorbide a a useful marker? Marine Ecology Progress Series **229**:33-42.

Ford, R. B., S. F. Thrush, and P. K. Probert. 1999. Macrobenthic colonisation of disturbances on an intertidal sandflat: The influence of season and buried algae. Marine Ecology Progress Series **191**:163-174.

Fox, S. E., M. Teichberg, Y. S. Olsen, L. Heffner, and I. Valiela. 2009. Restructuring of benthic communities in eutrophic estuaries: Lower abundance of prey leads to trophic shifts from omnivory to grazing. Marine Ecology Progress Series **380**:43-57.

France, R. L. and R. H. Peters. 1997. Ecosystem differences in the trophic enrichment of ^{13}C in aquatic food webs. Canadian Journal of Fisheries and Aquatic Sciences **54**:1255-1258.

Franke, U., L. Polerecky, E. Precht, and M. Huettel. 2006. Wave tank study of particulate organic matter degradation in permeable sediments. Limnology and Oceanography **51**:1084-1096.

Gambi, M. C., A. R. M. Nowell, and P. A. Jumars. 1990. Flume observations on flow dynamics in *Zostera-marina* (eelgrass) beds. Marine Ecology Progress Series **61**:159-169.

Gannes, L. Z., D. M. Obrien, and C. M. delRio. 1997. Stable isotopes in animal ecology: Assumptions, caveats, and a call for more laboratory experiments. Ecology **78**:1271-1276.

Gaston, K. J. 2000. Biodiversity: Higher taxon richness. Progress in Physical Geography **24**:117-127.

Gearing, P. J., J. N. Gearing, J. T. Maughan, and C. A. Oviatt. 1991. Isotopic distribution of carbon from sewage-sludge and eutrophication in the sediments and food web of estuarine ecosystems. Environmental Science & Technology **25**:295-301.

Geonet. 2011. Accessed 11 March 2013. www.geonet.org.nz.

Gibbs, M., G. Funnell, S. Pickmere, A. Norkko, and J. Hewitt. 2005. Benthic nutrient fluxes along an estuarine gradient: influence of the pinnid bivalve *Atrina zelandica* in summer. Marine Ecology Progress Series **288**:151-164.

Gibbs, P. E., G. W. Bryan, and P. L. Pascoe. 1991. Tbt-induced imposex in the dogwhelk, *Nucella-lapillus* - geographical uniformity of the response and effects. Marine Environmental Research **32**:79-87.

Giles, H. and C. A. Pilditch. 2006. Effects of mussel (*Perna canaliculus*) biodeposit decomposition on benthic respiration and nutrient fluxes. Marine Biology **150**:261-271.

Giller, P. S., H. Hillebrand, U. G. Berninger, M. O. Gessner, S. Hawkins, P. Inchausti, C. Inglis, H. Leslie, B. Malmqvist, M. T. Monaghan, P. J. Morin, and G. O'Mullan. 2004. Biodiversity effects on ecosystem functioning: Emerging issues and their experimental test in aquatic environments. Oikos **104**:423-436.

Gomez, I., F. L. Figueroa, P. Huovinen, N. Ulloa, and V. Morales. 2005. Photosynthesis of the red alga *Gracilaria chilensis* under natural solar radiation in an estuary in southern Chile. Aquaculture **244**:369-382.

Gonzalez, A. and M. Loreau. 2009. The causes and consequences of compensatory dynamics in ecological communities. Pages 393-414 Annual Review of Ecology Evolution and Systematics.

Graham, L. E., Wilcox, L.W. 2000. Algae. Prentice Hall, Upper Saddle River, New Jersey.

Grassle, J. F. and H. L. Sanders. 1973. Life histories and the role of disturbance. Dep Sea Research **20**:643-659.

Greenberg, C. H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. Forest Ecology and Management **148**:135-144.

Grilo, T. F., P. G. Cardoso, M. Dolbeth, and M. A. Pardal. 2009. Long-term changes in amphipod population dynamics in a temperate estuary following ecosystem restoration. Hydrobiologia **630**:91-104.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature **242**:344-347.

Guerra-Bobo, M. and T. E. Brough. 2011. Neighbour density, body size and anti-predator hiding time in the New Zealand mud-crab *Austrohelice crassa*. Journal of the Marine Biological Association of the United Kingdom **91**:691-694.

Hadwen, W. L. and A. H. Arthington. 2007. Food webs of two intermittently open estuaries receiving ^{15}N-enriched sewage effluent. Estuarine Coastal and Shelf Science **71**:347-358.

Hailes, S. F. 2006. Contribution of seagrass (*Zostera muelleri*) to estuarine food webs revealed by carbon and nitrogen stable isotope analysis. Unpub. MSc Thesis, University of Waikato, Hamilton, New Zealand. 105 pp.

Hall, S. J., D. Raffaelli, and S. F. Thrush. 1994. Patchiness and disturbance in shallow water benthic assemblages. Blackwell Scientific Publications.

Harvell, C. D., K. Kim, J. M. Burkholder, R. R. Colwell, P. R. Epstein, D. J. Grimes, E. E. Hofmann, E. K. Lipp, A. Osterhaus, R. M. Overstreet, J. W. Porter, G. W. Smith, and G. R. Vasta. 1999. Review: Marine ecology - Emerging marine diseases - Climate links and anthropogenic factors. Science **285**:1505-1510.

Hauxwell, J., J. Cebrian, and I. Valiela. 2006. Light dependence of *Zostera marina* annual growth dynamics in estuaries subject to different degrees of eutrophication. Aquatic Botany **84**:17-25.

Hayden, H. S., J. Blomster, C. A. Maggs, P. C. Silva, M. J. Stanhope, and J. R. Waaland. 2003. Linnaeus was right all along: *Ulva* and *Enteromorpha* are not distinct genera. European Journal of Phycology **38**:277-294.

Heckscher, E., J. Hauxwell, E. G. Jimenez, C. Rietsma, and I. Valiela. 1996. Selectivity by the herbivorous amphipod *Microdeutopus gryllotalpa* among five species of macroalgae. Biological Bulletin **191**:324-326.

Heip, C. H. R., N. K. Goosen, P. M. J. Herman, J. Kromkamp, J. J. Middelburg, and K. Soetaert. 1995. Production and consumption of biological particles in temperate tidal estuaries. Pages 1-149 *in* A. D. Ansell, R. N. Gibson, and M. Barnes, editors. Oceanography and Marine Biology - an Annual Review, Vol 33.

Herman, P. M. J., J. J. Middelburg, J. Van de Koppel, and C. H. R. Heip. 1999. Ecology of estuarine macrobenthos. Pages 195-240 *in* D. B. Nedwell and D. G. Raffaelli, editors. Advances in Ecological Research, Vol 29: Estuaries.

Hewitt, J., S. Thrush, M. Gibbs, D. Lohrer, and A. Norkko. 2006. Indirect effects of *Atrina zelandica* on water column nitrogen and oxygen fluxes: The role of benthic macrofauna and microphytes. Journal of Experimental Marine Biology and Ecology **330**:261-273.

Hickey, C. W. and M. M. Gibbs. 2009. Lake sediment phosphorus release management-Decision support and risk assessment framework. New Zealand Journal of Marine and Freshwater Research **43**:819-854.

Hinga, K. R., M. A. Arthur, M. E. Q. Pilson, and D. Whitaker. 1994. Carbon-isotope fractionation by marine-phytoplankton in culture - the effects of CO_2 concentration, pH, temperature, and species. Global Biogeochemical Cycles **8**:91-102.

Hobbs, R. J. and L. F. Huenneke. 1992. Disturbance, diversity, and invasion - Implications for conservations. Conservation Biology **6**:324-337.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics **4**:1-23.

Holmquist, J. G. 1994. Benthic macroalgae as a dispersal mechanism for fauna - Influence of a marine tumbleweed. Journal of Experimental Marine Biology and Ecology **180**:235-251.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs **75**:3-35.

Hopkinson, C. S., I. Buffam, J. Hobbie, J. Vallino, M. Perdue, B. Eversmeyer, F. Prahl, J. Covert, R. Hodson, M. A. Moran, E. Smith, J. Baross, B. Crump, S. Findlay, and K. Foreman. 1998. Terrestrial inputs of organic matter to coastal ecosystems: An intercomparison of chemical characteristics and bioavailability. Biogeochemistry **43**:211-234.

Howarth, R. W. 1988. Nutrient limitation of net primary production in marine ecosystems. Annual Review of Ecology and Systematics **19**:89-110.

Huang, T. L., J. L. Xu, and D. J. Cai. 2011. Efficiency of active barriers attaching biofilm as sediment capping to eliminate the internal nitrogen in eutrophic lake and canal. Journal of Environmental Sciences-China **23**:738-743.

Hughes, T. P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral-reef. Science **265**:1547-1551.

Hull, S. C. 1987. Macroalgal mats and species abundance - A field experiment. Estuarine Coastal and Shelf Science **25**:519-532.

Hume, T. M., Herdendorf, C.E. 1988. A geomorphic classification of estuaries and its application to coastal resource management - A New Zealand example. Ocean and Shoreline Management **11**.

Hurd, C. L., W. A. Nelson, R. Falshaw, and K. F. Neill. 2004. History, current status and future of marine macroalgal research in New Zealand: Taxonomy, ecology, physiology and human uses. Phycological Research **52**:80-106.

Huston, M. 1979. General hypothesis of species-diversity. American Naturalist **113**:81-101.

Hutt, S. D. 2012. First responders to cataclysmic upheaval: Earthquake–driven effects on microalgae in the Avon-Heathcote Estuary, Christchurch, New Zealand. University of Canterbury.

Inglis, G. J. 2003. The seagrasses of New Zealand. University of California Press, Berkley.

Irlandi, E. A. and M. K. Crawford. 1997. Habitat linkages: The effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. Oecologia **110**:222-230.

Ishihi, Y. 2003. Feeding of the bivalve *Theora lubrica* on benthic microalgae: Isotopic evidence. Marine Ecology Progress Series **255**:303-309.

Jacobs, P. H. and U. Forstner. 1999. Concept of subaqueous capping of contaminated sediments with active barrier systems (ABS) using natural and modified zeolites. Water Research **33**:2083-2087.

James, R. J., M. P. L. Smith, and P. G. Fairweather. 1995. Sieve mesh size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. Marine Ecology Progress Series **118**:187-198.

Jephson, T., P. Nystrom, P.-O. Moksnes, and S. P. Baden. 2008a. Trophic interactions in *Zostera marina* beds along the Swedish coast. Marine Ecology Progress Series **369**:63-76.

Jephson, T., P. Nystrom, P. O. Moksnes, and S. P. Baden. 2008b. Trophic interactions in *Zostera marina* beds along the Swedish coast. Marine Ecology Progress Series **369**:63-76.

Jesus, B., Brotas, V., Ribeiro, L., Mendes, C.R., Cartaxana, P., Paterson, D.M. 2009. Adaptations of microphytobenthos assemblages to sediment type and tidal position. Continental Shelf Research **29**:1624-1634.

Johnson, R. G. 1973. Conceptual models of benthic communities Freeman Cooper and Co., San Francisco.

Jones, A. R. 1986. The effects of dredging and spoil disposal on macrobenthos, Hawkesbury Estuary, NSW. Marine Pollution Bulletin **17**:17-20.

Jones, G. and S. Candy. 1981. Effects of dredging on the macrobenthic infauna of Botany Bay. Australian Journal of Marine and Freshwater Research **32**:379-398.

Jones, H. F. E., C. A. Pilditch, D. A. Bruesewitz, and A. M. Lohrer. 2011. Sedimentary environment influences the effect of an infaunal suspension feeding bivalve on estuarine ecosystem function. Plos One **6**.

Jones, H. P. and O. J. Schmitz. 2009. Rapid recovery of damaged ecosystems. Plos One **4**.

Jones, J., R. D. DeBruyn, J. J. Barg, and R. J. Robertson. 2001. Assessing the effects of natural disturbance on a neotropical migrant songbird. Ecology **82**:2628-2635.

Jones, J. B. 1992. Environmental-impact of trawling on the seabed - a review. New Zealand Journal of Marine and Freshwater Research **26**:59-67.

Jones, M. B. and M. J. Simons. 1983. Latitudinal variation in reproductive characteristics of a mud crab, *Helice-crassa* (grapsidae). Bulletin of Marine Science **33**:656-670.

Jones, M. B., Simons, M.J. . 1982. Habitat preferences of two estuarine burrowing crabs *Helice crassa* Dana (Grapsidae) and *Macrophthalmus hirtipes* (Jacquinot) (Ocypodidae). Journal of Experimental Marine Biology and Ecology **56**.

Jones, T. C., C. E. C. Gemmill, and C. A. Pilditch. 2008. Genetic variability of New Zealand seagrass (*Zostera muelleri*) assessed at multiple spatial scales. Aquatic Botany **88**:39-46.

Josefson, A. B. 1990. Increase of benthic biomass in the Skagerrak-Kattegat during the 1970s and 1980s - Effects of organic enrichment. Marine Ecology Progress Series **66**:117-130.

Juniper, K. 1982. Regulation of microbial production in intertidal mudflats - the role of *Amphibola crenata*, a deposit feeding gastropod. PhD Thesis, University of Canterbury, New Zealand.

Juniper, K. 1987. Deposit feeding ecology of *Amphibola crenata* 1. Long-term effects of deposit feeding on sediment micro-organisms. New Zealand Journal of Marine and Freshwater Research **21**:235-246.

Kang, C.-K., Y.-W. Lee, E. J. Choy, J.-K. Shin, I.-S. Seo, and J.-S. Hong. 2006. Microphytobenthos seasonality determines growth and reproduction in intertidal bivalves. Marine Ecology Progress Series **315**:113-127.

Kang, C. K., J. B. Kim, K. S. Lee, J. B. Kim, P. Y. Lee, and J. S. Hong. 2003. Trophic importance of benthic microalgae to macrozoobenthos in coastal bay systems in Korea: Dual stable C and N isotope analyses. Marine Ecology Progress Series **259**:79-92.

Kaplan, E. H., Welker, J.R., Kraus, M.G., McCourt, S. 1975. Some factors affecting the colonization of a dredged channel. Marine Biology **32**:193-204.

Kapusta, S. C., Bemvenutti, C.E. 1998. Atividade nictimeral de alimentação de juvenis de Callinectes sapidus , Rathbun, 1895 (Decapoda, Portunidae) numa pradaria de Rippia maritima L. e num plano não vegetado, numa enseada estuarina da Lagoa dos Patos, R.S., Brasil. Nauplius **6**:41-52.

Kauppila, P., K. Weckstrom, S. Vaalgamaa, A. Korhola, H. Pitkanen, N. Reuss, and S. Drew. 2005. Tracing pollution and recovery using sediments in an urban estuary, northern Baltic Sea: Are we far from ecological reference conditions? Marine Ecology Progress Series **290**:35-53.

Keats, R. A., L. J. Osher, and H. A. Neckers. 2004. The effect of nitrogen loading on a brackish estuarine faunal community: A stable isotope approach. Estuaries **27**:460-471.

Ketchum, B. H. 1983. Estuarine characteristics. Pages 1-14 *in* B. H. Ketchum, editor. Estuaries and enclosed seas. Ecosystems of the world 26. Elsevier, New York.

Kikuchi, T. 1979. Some aspects of ecology, life cycle and taxonomy of the polychaete *Capitella capitata*, so called pollution indicator: a review. Benthos Research **17/18**.

Killops, S., Killops, V. 2005. An introduction to organic geochemistry. Second Edition. John Wiley & Sons, Incorporated.

Kim, G., W. Jeong, S. Choi, and J. Khim. 2007. Sand capping for controlling phosphorus release from lake sediments. Environmental Technology **28**:381-389.

Kinney, E. H. and C. T. Roman. 1998. Response of primary producers to nutrient enrichment in a shallow estuary. Marine Ecology Progress Series **163**:89-98.

Kitamori, R. 1975. Benthos as a environmental indicator (S) with special reference to indicator species Pages 265-273 The special committee of Japanese Ecological Society on environmental prodlems (ed.) Kankyo to Seibutsu Shihyo (Envrionment and Indicator Species). Aquatic Environment. Kyoritsu Shuppan, Tokyo.

Knox, G. A., Kilner, A.R. 1973. The ecology of the Avon-Heathcote Estuary. Unpublished report to the Christchurch Drainage Board by the Estuarine Reserach Unit, Department of Zoology, University of Canterbury. 358pp.

Korb, R. E., J. A. Raven, A. M. Johnston, and J. W. Leftley. 1996. Effects of cell size and specific growth rate on stable carbon isotope discrimination by two species of marine diatom. Marine Ecology Progress Series **143**:283-288.

Koroleff, F. 1983. Determination of ammonia.*in* K. Grasshoff, Ehrhardt, M., Kremling, K., editor. Methods of seawater analysis, Verlag Chemie, Weihneim.

Kristensen, E. 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. Journal of Sea Research **59**:30-43.

Kubler, J. E. and J. A. Raven. 1995. The interaction between inorganic carbon acquisition and light supply in *Palmaria-palmata* (Rhodophyta). Journal of Phycology **31**:369-375.

Kurata, K., H. Minami, and E. Kikuchi. 2001. Stable isotope analysis of food sources for salt marsh snails. Marine Ecology Progress Series **223**:167-177.

Lai, Y.-C., B.-S. Shieh, and Y.-C. Kam. 2007. Population patterns of a riparian frog (*Rana swinhoana*) before and after an earthquake in subtropical Taiwan. Biotropica **39**:731-736.

Lapointe, B. E., P. J. Barile, M. M. Littler, and D. S. Littler. 2005. Macroalgal blooms on southeast Florida coral reefs II. Cross-shelf discrimination of nitrogen sources indicates widespread assimilation of sewage nitrogen. Harmful Algae **4**:1106-1122.

Lapointe, B. E. and K. R. Tenore. 1981. Experimental outdoor studies with *Ulva-fasciata Delile* .1. Interaction of light and nitrogen on nutrient-uptake, growth, and biochemical-composition. Journal of Experimental Marine Biology and Ecology **53**:135-152.

Lapointe, B. E., K. Thacker, C. Hanson, and L. Getten. 2011. Sewage pollution in Negril, Jamaica: Effects on nutrition and ecology of coral reef macroalgae. Chinese Journal of Oceanology and Limnology **29**:775-789.

Lardicci, C., S. Como, S. Corti, and F. Rossi. 2001. Recovery of the macrozoobenthic community after severe dystrophic crises in a Mediterranean coastal lagoon (Orbetello, Italy). Marine Pollution Bulletin **42**:202-214.

Larsen, C. P. S. and G. M. Macdonald. 1993. Lake morphometry, sediment mixing and the selection of sites for fine resolution paleoecological studies. Quaternary Science Reviews **12**:781-792.

Larson, F. and K. Sundback. 2008. Role of microphytobenthos in recovery of functions in a shallow-water sediment system after hypoxic events. Marine Ecology Progress Series **357**:1-16.

Lawton, J. H. 1994. What do species do in ecosystems. Oikos **71**:367-374.

Lebednik, P. A. 1973. Ecological effects of intertidal uplifting from nuclear testing. Marine Biology **20**:197-207.

Leduc, D., P. K. Probert, R. D. Frew, and C. L. Hurd. 2006. Macroinvertebrate diet in intertidal seagrass and sandflat communities: A study using C, N, and S stable isotopes. New Zealand Journal of Marine and Freshwater Research **40**:615-629.

Lee, K. M., S. Y. Lee, and R. M. Connolly. 2011. Short-term response of estuarine sandflat trophodynamics to pulse anthropogenic physical disturbance: Support for the Intermediate Disturbance Hypothesis. Estuarine Coastal and Shelf Science **92**:639-648.

Lee, S. Y. 2000. Carbon dynamics of Deep Bay, eastern Pearl River estuary, China. II: Trophic relationship based on carbon- and nitrogen-stable isotopes. Marine Ecology Progress Series **205**:1-10.

Les, D. H., M. L. Moody, S. W. L. Jacobs, and R. J. Bayer. 2002. Systematics of seagrasses (Zosteraceae) in Australia and New Zealand. Systematic Botany **27**:468-484.

Lillebo, A. I., J. M. Neto, I. Martins, T. Verdelhos, S. Leston, P. G. Cardoso, S. M. Ferreira, J. C. Marques, and M. A. Pardal. 2005. Management of a shallow temperate estuary to control eutrophication: The effect of hydrodynamics on the system's nutrient loading. Estuarine Coastal and Shelf Science **65**:697-707.

Little, C. 2000. The biology of soft shores and estuaries. Oxford University Press.

Little, C., P. Stirling, M. Pilkington, and J. Pilkington. 1985. Larval development and metamorphosis in the marine pulmonate *Amphibola-crenata* (Mollusca, Pulmonata). Journal of Zoology **205**:489-510.

Lohrer, A. M., N. J. Halliday, S. F. Thrush, J. E. Hewitt, and I. F. Rodil. 2010. Ecosystem functioning in a disturbance-recovery context: Contribution of

macrofauna to primary production and nutrient release on intertidal sandflats. Journal of Experimental Marine Biology and Ecology **390**:6-13.

Lohrer, A. M., S. F. Thrush, and M. M. Gibbs. 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature **431**:1092-1095.

Lohrer, A. M., S. F. Thrush, L. Hunt, N. Hancock, and C. Lundquist. 2005. Rapid reworking of subtidal sediments by burrowing spatangoid urchins. Journal of Experimental Marine Biology and Ecology **321**:155-169.

Lohrer, A. M., M. Townsend, I. F. Rodil, J. E. Hewitt, and S. F. Thrush. 2012. Detecting shifts in ecosystem functioning: The decoupling of fundamental relationships with increased pollutant stress on sandflats. Marine Pollution Bulletin **64**:2761-2769.

Lohrer, A. M. and J. J. Wetz. 2003. Dredging-induced nutrient release from sediments to the water column in a southeastern saltmarsh tidal creek. Marine Pollution Bulletin **46**:1156-1163.

Lopez, G. R. and J. S. Levinton. 1987. Ecology of deposit-feeding animals in marine-sediments. Quarterly Review of Biology **62**:235-260.

Loreau, M. 2004. Does functional redundancy exist? Oikos **104**:606-611.

Loreau, M. and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature **412**:72-76.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Ecology - biodiversity and ecosystem functioning: Current knowledge and future challenges. Science **294**:804-808.

Lorenzen, J., L. H. Larsen, T. Kjaer, and N. P. Revsbech. 1998. Biosensor determination of the microscale distribution of nitrate, nitrate assimilation, nitrification, and denitrification in a diatom-inhabited freshwater sediment. Applied and Environmental Microbiology **64**:3264-3269.

Lotze, H. K. and I. Milewski. 2004. Two centuries of multiple human impacts and successive changes in a North Atlantic food web. Ecological Applications **14**:1428-1447.

Luoma, S. N. 1989. Can we determine the biological availability of sediment-bound trace-elements. Hydrobiologia **176**:379-396.

Lynch, J. F. 1991. Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. Biotropica **23**:488-496.

Maa, C. J. W., H. J. Wang, and H. J. Lin. 2006. Impacts of catastrophic earthquakes on the insect communities in estuarine mangroves, Northern Taiwan. Biodiversity and Conservation **15**:429-441.

Machas, R., R. Santos, and B. Peterson. 2003. Tracing the flow of organic matter from primary producers to filter feeders in Ria Formosa lagoon, southern Portugal. Estuaries **26**:846-856.

MacIntyre, H. L., R. J. Geider, and D. C. Miller. 1996. Microphytobenthos: The ecological role of the "secret garden" of unvegetated, shallow-water marine habitats .1. Distribution, abundance and primary production. Estuaries **19**:186-201.

Mallela, J. and C. Harrod. 2008. Delta C-13 and delta N-15 reveal significant differences in the coastal foodwebs of the seas surrounding Trinidad and Tobago. Marine Ecology Progress Series **368**:41-51.

Marcuson, W. F. 1978. Definition of terms related to liquefaction. Journal of Geotechnical Engineering Division, ASCE **104**:1197-1200.

Marsh, A. G. and K. R. Tenore. 1990. The role of nutrition in regulating the population-dynamics of opportunistic, surface deposit feeders in a mesohaline community. Limnology and Oceanography **35**:710-724.

Martinetto, P., M. Teichberg, and I. Valiela. 2006. Coupling of estuarine benthic and pelagic food webs to land-derived nitrogen sources in Walquoit Bay, Massachusetts, USA. Marine Ecology Progress Series **307**:37-48.

Mazia, C., E. J. Chaneton, M. Machera, A. Uchitel, M. V. Feler, and C. M. Ghersa. 2010. Antagonistic effects of large- and small-scale disturbances on exotic tree invasion in a native tussock grassland relict. Biological Invasions **12**:3109-3122.

McClelland, J. W. and I. Valiela. 1998. Linking nitrogen in estuarine producers to land-derived sources. Limnology and Oceanography **43**:577-585.

McIntire, C. D. and M. C. Amspoker. 1986. Effects of sediment properties on benthic primary production in the Columbia River Estuary. Aquatic Botany **24**:249-267.

Mclay, C. 1976. An inventory of the status and origin of New Zealand estuarine systems. Proceedings of the New Zealand Ecological Society **23**.

Mclusky, D. S. 1981. The estuarine ecosystem. Blackie, Glasgow.

McNaughton, S. J. 1977. Diversity and stability of ecological communities - comment on role of empiricism in ecology. American Naturalist **111**:515-525.

Measures, R., Hicks, M., Shankar, U., Bind, J., Arnold, J. Zeldis, J. 2011. Mapping earthquake induced topographic change and liquefaction in the Avon-Heathcote Estuary. National Institute of Water and Atmospheric Research, Christchurch, New Zealand.

Meysman, F. J. R., J. J. Middelburg, and C. H. R. Heip. 2006. Bioturbation: A fresh look at Darwin's last idea. Trends in Ecology & Evolution **21**:688-695.

Middelburg, J. J., C. Barranguet, H. T. S. Boschker, P. M. J. Herman, T. Moens, and C. H. R. Heip. 2000. The fate of intertidal microphytobenthos carbon: An *in situ* C-13-labeling study. Limnology and Oceanography **45**:1224-1234.

Middelburg, J. J. and L. A. Levin. 2009. Coastal hypoxia and sediment biogeochemistry. Biogeosciences **6**:1273-1293.

Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. American Naturalist **120**:533-536.

Miura, O., Y. Sasaki, and S. Chiba. 2012. Destruction of populations of *Batillaria attramentaria* (Caenogastropoda: Batillariidae) by tsunami waves of the 2011 Tohoku earthquake. Journal of Molluscan Studies **78**:377-380.

Molino, J. F. and D. Sabatier. 2001. Tree diversity in tropical rain forests: A validation of the intermediate disturbance hypothesis. Science **294**:1702-1704.

Montgomery, J. R., C. F. Zimmermann, and M. T. Price. 1979. Collection, analysis and variation of nutrients in estuarine pore water. Estuarine and Coastal Marine Science **9**:203-214.

Montserrat, F., C. Van Colen, S. Degraer, T. Ysebaert, and P. M. J. Herman. 2008. Benthic community-mediated sediment dynamics. Marine Ecology Progress Series **372**:43-59.

Mook, W. G., Tan, F.C. 1991. Stable carbon isotopes in rivers and estuaries.*in* E. T. Degens, Kempe, S. Richey, J., editor. Biogeochemistry of major world rivers. John Wiley, Chichester.

Moore, D. C. and G. K. Rodger. 1991. Recovery of a sewage-sludge dumping ground .2. Macrobenthic community. Marine Ecology Progress Series **75**:301-308.

Morris, D. V. 1983. A note on earthquake-induced liquefaction. Geotechnique **33**:451-454.

Morrisey, D. J. 1988. Differences in effects of grazing by deposit-feeders *hydrobia-ulvae* (Pennant) (Gastropoda, Prosobranchia) and *corophium-arenarium* Crawford (Amphipoda) on sediment microalgal populations .2. Quantitative effects. Journal of Experimental Marine Biology and Ecology **118**:43-53.

Morton, J. E., Miller, M.C. 1968. The New Zealand sea shore. Collins, Auckland.

Morton, J. E., Miller, M.C. 1973. The New Zealand Sea Shore. 2nd Edition edition. Collins, London.

Munari, C., S. Modugno, F. Ghion, G. Castaldelli, E. A. Fano, R. Rossi, and M. Mistri. 2003. Recovery of the macrobenthic community in the Valli di Comacchio, northern Adriatic Sea, Italy. Oceanologica Acta **26**:67-75.

Naeem, S. 2002. Ecosystem consequences of biodiversity loss: The evolution of a paradigm. Ecology **83**:1537-1552.

Naeem, S., Bunker, D.E., Hector, A., Loreau, M., Perrings, C. 2009. Biodiversity, ecosystem functioning and human well-being: An ecological and economic perspective. Oxford University Press.

Needham, H. R., C. A. Pilditch, A. M. Lohrer, and S. F. Thrush. 2010. Habitat dependence in the functional traits of *austrohelice crassa,* a key bioturbating species. Marine Ecology Progress Series **414**:179-193.

Needham, H. R., C. A. Pilditch, A. M. Lohrer, and S. F. Thrush. 2011. Context-specific bioturbation mediates changes to ecosystem functioning. Ecosystems **14**:1096-1109.

Needoba, J. A., D. M. Sigman, and P. J. Harrison. 2004. The mechanism of isotope fractionation during algal nitrate assimilation as illuminated by the $^{15}N/^{14}N$ of intracellular nitrate. Journal of Phycology **40**:517-522.

Newell, R. C. 1979. Biology of intertidal animals. Faversham, UK: Marine Ecological Surveys.

Nilsson, C. and K. Sundback. 1991. Growth and nutrient-uptake studied in sand-agar microphytobenthic communities. Journal of Experimental Marine Biology and Ecology **153**:207-226.

Nixon, S. W. 1995. Coastal marine eutrophication - a definition, social causes, and future concerns. Ophelia **41**:199-219.

Norkko, J., E. Bonsdorff, and A. Norkko. 2000. Drifting algal mats as an alternative habitat for benthic invertebrates: Species specific responses to a transient resource. Journal of Experimental Marine Biology and Ecology **248**:79-104.

Norling, K., R. Rosenberg, S. Hulth, A. Gremare, and E. Bonsdorff. 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. Marine Ecology Progress Series **332**:11-23.

O'Leary, M. H. 1988. Carbon isotope fractionation during photosynthesis. BioScience **38**:328.

Oczkowski, A., S. Nixon, K. Henry, P. DiMilla, M. Pilson, S. Granger, B. Buckley, C. Thornber, R. McKinney, and J. Chaves. 2008. Distribution and trophic importance of anthropogenic nitrogen in Narragansett Bay: An assessment using stable isotopes. Estuaries and Coasts **31**:53-69.

Odum, E. P. 1985. Trends expected in stressed ecosystems. BioScience **35**:419-422.

Olsen, Y. S., S. E. Fox, M. Teichberg, M. Otter, and I. Valiela. 2011. Delta N-15 and delta C-13 reveal differences in carbon flow through estuarine benthic food

webs in response to the relative availability of macroalgae and eelgrass. Marine Ecology Progress Series **421**:83-96.

Olsgard, F., T. Brattegard, and T. Holthe. 2003. Polychaetes as surrogates for marine biodiversity: Lower taxonomic resolution and indicator groups. Biodiversity and Conservation **12**:1033-1049.

Osman, R. W. 1977. The establishment and development of a marine epifaunal community. Ecological Monographs **47**:37-63.

Owen, J. 1992. The estuary: Where our rivers meet the sea. Christchurch City Council, Christchurch, New Zealand.

Padisak, J. 1993. The influence of different disturbance frequencies on the species richness, diversity and equitability of phytoplankton in shallow lakes. Hydrobiologia **249**:135-156.

Paerl, H. W. 1997. Coastal eutrophication and harmful algal blooms: Importance of atmospheric deposition and groundwater as "new" nitrogen and other nutrient sources. Limnology and Oceanography **42**:1154-1165.

Park, R., Epstein, S. 1961. Metabolic fractionation of ^{13}C and ^{12}C in plants. Plant Physiology **36**:133-138.

Parsons, T. R., Maita, Y., Lalli, C.M. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford.

Paterson, D. M. and S. E. Hagerthey. 2001. Microphytobenthos in contrasting coastal ecosystems: Biology and dynamics. Ecological Comparisons of Sedimentary Shores **151**:105-125.

Paterson, D. M., Wiltshire, K.H., Miles, A., Blackburn, J., Davidson, I., Yates, M.G., McGrorty, S., Eastwood, J.A. 1998. Microbial meditation of spectral reflectance from intertidal cohesive sediments. Limnology and Oceanography **43**:1207-1221.

Pearson, T. H. and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology Annual Review **16**:229-311.

Peletier, H. 1996. Long-term changes in intertidal estuarine diatom assemblages related to reduced input of organic waste. Marine Ecology Progress Series **137**:265-271.

Perillo, G. M. E. 1995. Definitions and geomorphologic classifications of estuaries.*in* G. M. E. Perillo, editor. Geomorphology and sedimentology of estuaries. Developments in sedimentology 53. Elsevier Science, Amsterdam.

Peters, K. E., R. E. Sweeney, and I. R. Kaplan. 1978. Correlation of carbon and nitrogen stable isotope ratios in sedimentary organic-matter. Limnology and Oceanography **23**:598-604.

Peterson, B. J. and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics **18**:293-320.

Peterson, B. J. and R. W. Howarth. 1987. Sulfur, carbon, and nitrogen isotopes used to trace organic-matter flow in the salt-marsh estuaries of Sapelo Island, Georgia. Limnology and Oceanography **32**:1195-1213.

Peterson, C. H. 1982. Clam predation by whelks (*Busycon* spp) - Experimental tests of the importance of prey size, prey density, and seagrass cover. Marine Biology **66**:159-170.

Peterson, C. H., H. C. Summerson, and P. B. Duncan. 1984. The influence of seagrass cover on population-structure and individual growth-rate of a suspension-feeding bivalve, *Mercenaria-mercenaria*. Journal of Marine Research **42**:123-138.

Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. Ecosystems **1**:6-18.

Phillips, D. L. and J. W. Gregg. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia **127**:171-179.

Pilkington, M. C. and J. B. Pilkington. 1982. The planktonic veliger of *Amphibola-crenata* (Gmelin). Journal of Molluscan Studies **48**:24-29.

Pomeroy, L. R. 1959. Algal productivity in salt marshes of Georgia. Limnology and Oceanography **4**:386-397

Posey, M. H. 1990. Functional approaches to soft-substrate communities - How useful are they? Reviews in Aquatic Sciences **2**:343-356.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology **83**:703-718.

Prathep, A., J. Mayakun, P. Tantiprapas, and A. Darakrai. 2008. Can macroalgae recover, 13 months after the 2004 Tsunami?: A case study at Talibong Island, Trang Province, Thailand. Journal of Applied Phycology **20**:907-914.

Pruell, R. J., B. K. Taplin, J. L. Lake, and S. Jayaraman. 2006. Nitrogen isotope ratios in estuarine biota collected along a nutrient gradient in Narragansett Bay, Rhode Island, USA. Marine Pollution Bulletin **52**:612-620.

Pulgar, J., M. Aldana, E. Vergara, and M. GeorgeNascimento. 1995. Behavior of the estuarine crab *Hemigrapsus crenulatus* (Milne-Edwards 1837) in relation to the parasitism by the acanthocephalan *Profilicollis antarcticus* (Zdzitowiecki 1985) in southern Chile. Revista Chilena De Historia Natural **68**:439-450.

Raffaelli, D. 1992. Conservation of Scottish estuaries. Proceedings of the Royal Society of Edinburgh Section B-Biological Sciences **100**:55-76.

Raffaelli, D., Hawkins, S. 1996. Intertidal Ecology. Chapman and Hall, London.

Raffaelli, D. G. 2006. Biodiversity and ecosystem functioning: issues of scale and trophic complexity. Marine Ecology Progress Series **311**:285-294.

Rainey, M. P., A. N. Tyler, D. J. Gilvear, R. G. Bryant, and P. McDonald. 2003. Mapping intertidal estuarine sediment grain size distributions through airborne remote sensing. Remote Sensing of Environment **86**:480-490.

Rau, G. H., R. E. Sweeney, I. R. Kaplan, A. J. Mearns, and D. R. Young. 1981. Differences in animal ^{13}C, ^{15}N and abundance between a polluted and an unpolluted coastal site - likely indicators of sewage uptake by a marine food web. Estuarine Coastal and Shelf Science **13**:701-707.

Raven, J. A., A. M. Johnston, J. E. Kubler, R. Korb, S. G. McInroy, L. L. Handley, C. M. Scrimgeour, D. I. Walker, J. Beardall, M. Vanderklift, S. Fredriksen, and K. H. Dunton. 2002. Mechanistic interpretation of carbon isotope discrimination by marine macroalgae and seagrasses. Functional Plant Biology **29**:355-378.

Reagan, D. P. 1991. The response of Anolis lizards to hurricane-induced habitat changes in a Puerto-Rican rain-forest. Biotropica **23**:468-474.

Retamal, M. A. 2000. Decapodos en Chile. ETI (Ed.), World Biodiversity., University of Amsterdam, Amsterdam.

Riznyk, R. Z. and H. K. Phinney. 1972. Manometric assessment of interstitial microalgae production in 2 estuarine sediments. Oecologia **10**:193-&.

Robertson, B., Stevens, L. 2006. Southland estuaries state of environment report 2001-2006. Prepared for Environment Southland. 45p.

Robertson, B. M., Gillespie, P.A., Asher, R.A., Frisk, S., Keeley, N.B., Hopkins, G.A., Thompson, S.J., Tuckey, B.J. . 2002. Estuarine Environmental Assessment and Monitoring: A National Protocol. Part A. Development, Part B. Appendices, and Part C. Application. Prepared for supporting Councils and

the Ministry for the Environment, Sustainable Management Fund Contract No. 5096. Part A. 93p. Part B. 159p. Part C. 40p plus field sheets.

Rodil, I. F., A. M. Lohrer, L. D. Chiaroni, J. E. Hewitt, and S. F. Thrush. 2011. Disturbance of sandflats by thin terrigenous sediment deposits: consequences for primary production and nutrient cycling. Ecological Applications **21**:416-426.

Rogers, K. M. 1999. Effects of sewage contamination on macro-algae and shellfish at Moa Point, New Zealand using stable carbon and nitrogen isotopes. New Zealand Journal of Marine and Freshwater Research **33**:181-188.

Rogers, K. M. 2003. Stable carbon and nitrogen isotope signatures indicate recovery of marine biota from sewage pollution at Moa Point, New Zealand. Marine Pollution Bulletin **46**:821-827.

Romme, W. H., E. H. Everham, L. E. Frelich, M. A. Moritz, and R. E. Sparks. 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? Ecosystems **1**:524-534.

Rosenberg, G. and J. Ramus. 1982. Ecological growth strategies in the seaweeds *Gracilaria-foliifera* (Rhodophyceae) and *Ulva* sp (Chlorophyceae) - soluble nitrogen and reserve carbohydrates. Marine Biology **66**:251-259.

Rosenberg, R., L. O. Loo, and P. Moller. 1992. Hypoxia, salinity and temperature as structuring factors for marine benthic communities in a eutrophic area. Netherlands Journal of Sea Research **30**:121-129.

Ross, P. M., I. D. Hogg, C. A. Pilditch, C. J. Lundquist, and R. J. Wilkins. 2012. Population genetic structure of the New Zealand estuarine clam *Austrovenus stutchburyi* (Bivalvia: Veneridae) reveals population subdivision and partial congruence with biogeographic boundaries. Estuaries and Coasts **35**:143-154.

Rossi, F., M. Vos, and J. J. Middelburg. 2009. Species identity, diversity and microbial carbon flow in reassembling macrobenthic communities. Oikos **118**:503-512.

Round, F. E. 1971. Benthic marine diatoms. Oceanography and Marine Biology Annual Review **9**:83-139.

Sackett, W. M., Eckelman.Wr, M. L. Bender, and A. W. H. Be. 1965. Temperature dependence of carbon isotope composition in marine plankton and sediments. Science **148**:235-&.

Sakamaki, T. and J. S. Richardson. 2008. Effects of small rivers on chemical properties of sediment and diets for primary consumers in estuarine tidal flats. Marine Ecology Progress Series **360**:13-24.

Sakamaki, T. and J. S. Richardson. 2009. Dietary responses of tidal flat macrobenthos to reduction of benthic microalgae: A test for potential use of allochthonous organic matter. Marine Ecology Progress Series **386**:107-113.

Salo, J., R. Kalliola, I. Hakkinen, Y. Makinen, P. Niemela, M. Puhakka, and P. D. Coley. 1986. River dynamics and the diversity of Amazon lowland forest. Nature **322**:254-258.

Sandwell, D. R., C. A. Pilditch, and A. M. Lohrer. 2009. Density dependent effects of an infaunal suspension-feeding bivalve (*Austrovenus stutchburyi*) on sandflat nutrient fluxes and microphytobenthic productivity. Journal of Experimental Marine Biology and Ecology **373**:16-25.

Sartory, D. P. and J. U. Grobbelaar. 1984. Extraction of chlorophyll-a from fresh-water phytoplankton for spectrophotometric analysis. Hydrobiologia **114**:177-187.

Sathianandan, T. V., K. S. Mohamed, and E. Vivekanandan. 2012. Species diversity in fished taxa along the southeast coast of India and the effect of the Asian Tsunami of 2004. Marine Biodiversity **42**:179-187.

Sauriau, P. G. and C. K. Kang. 2000. Stable isotope evidence of benthic microalgae-based growth and secondary production in the suspension feeder *Cerastoderma edule* (Mollusca, Bivalvia) in the Marennes-Oleron Bay. Hydrobiologia **440**:317-329.

Savage, C. and R. Elmgren. 2004. Macroalgal (*Fucus vesiculosus*) delta15-N values trace decrease in sewage influence. Ecological Applications **14**:517-526.

Savage, C., R. Elmgren, and U. Larsson. 2002. Effects of sewage-derived nutrients on an estuarine macrobenthic community. Marine Ecology Progress Series **243**:67-82.

Scheibling, R. E., C. Feehan, and J. S. Lauzon-Guay. 2010. Disease outbreaks associated with recent hurricanes cause mass mortality of sea urchins in Nova Scotia. Marine Ecology Progress Series **408**:109-116.

Schiel, D. R. 2006. Rivets or bolts? When single species count in the function of temperate rocky reef communities. Journal of Experimental Marine Biology and Ecology **338**:233-252.

Schiel, D. R. and W. A. Nelson. 1990. The harvesting of macroalgae in New Zealand. Hydrobiologia **204**:25-33.

Schwartz, M. L. 2005. Encyclopedia of coastal science. Springer, The Netherlands.

Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. van Mantgem. 2000. Linking biodiversity to ecosystem function: Implications for conservation ecology. Oecologia **122**:297-305.

Shaffer, G. P. and C. P. Onuf. 1983. An analysis of factors influencing the primary production of the benthic microflora in a Southern-California lagoon. Netherlands Journal of Sea Research **17**:126-144.

Short, F. T., D. M. Burdick, and J. E. Kaldy. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera-marina*. Limnology and Oceanography **40**:740-749.

Short, F. T. and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation **23**:17-27.

Shumway, S. E., Barter, J., Schick, D.E. 1987. Food resources related to habitat in the scallop *Placopecten magellanicus* (Gmelin). Journal of Shellfish Research **7**:77-82.

Shurin, J. B., D. S. Gruner, and H. Hillebrand. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. Proceedings of the Royal Society B-Biological Sciences **273**:1-9.

Simenstad, C., D. Reed, and M. Ford. 2006. When is restoration not? Incorporating landscape-scale processes to restore self-sustaining ecosystems in coastal wetland restoration. Ecological Engineering **26**:27-39.

Simenstad, C. A. and R. C. Wissmar. 1985. Delta-C-13 evidence of the origins and fates of organic-carbon in estuarine and nearshore food webs. Marine Ecology Progress Series **22**:141-152.

Singer, G. A. and T. J. Battin. 2007. Anthropogenic subsidies alter stream consumer-resource stoichiometry, biodiversity, and food chains. Ecological Applications **17**:376-389.

Smith, M. D. and A. K. Knapp. 2003. Dominant species maintain ecosystem function with non-random species loss. Ecology Letters **6**:509-517.

Smith, V. H., G. D. Tilman, and J. C. Nekola. 1999. Eutrophication: Impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environmental Pollution **100**:179-196.

Snelgrove, P., T. H. Blackburn, P. A. Hutchings, D. M. Alongi, J. F. Grassle, H. Hummel, G. King, I. Koike, P. J. D. Lambshead, N. B. Ramsing, and V. Solis-Weiss. 1997. The importance of marine sediment biodiversity in ecosystem precesses. Ambio **26**:578-583.

Sousa, W. P. 1979. Disturbance in marine inter-tidal boulder fields - the non-equilibrium maintenance of species-diversity. Ecology **60**:1225-1239.

Southward, A. J. 1995. The importance of long time-series in understanding the variability of natural systems. Helgolander Meeresuntersuchungen **49**:329-333.

Spies, R. B., H. Kruger, R. Ireland, and D. W. Rice. 1989. Stable isotope ratios and contaminant concentrations in a sewage-distorted food web. Marine Ecology Progress Series **54**:157-170.

Stephenson, R. L. 1981. Aspects of the energetics of the cockle *Chione* (*Austrovenus*) *stutchburyi* in the Avon-Heathcote Estuary, Christchurch, New Zealand. Unversity of Canterbury.

Stephenson, R. L. and P. E. Chanley. 1979. Larval development of the cockle *Chione stutchburyi* (Bivalvia Veneridae) reared in the laboratory. New Zealand Journal of Zoology **6**:553-560.

Sterk, M., G. Gort, A. Klimkowska, J. van Ruijven, A. J. A. van Teeffelen, and G. W. W. Wamelink. 2013. Assess ecosystem resilience: Linking response and effect traits to environmental variability. Ecological Indicators **30**:21-27.

Stoner, A. W. 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. Bulletin of Marine Science **30**:537-551.

Sullivan, M. J. and C. A. Moncreiff. 1990. Edaphic algae are an important component of salt-marsh food-webs - evidence from multiple stable isotope analyses. Marine Ecology Progress Series **62**:149-159.

Sundback, K., A. Miles, and E. Goransson. 2000. Nitrogen fluxes, denitrification and the role of microphytobenthos in microtidal shallow-water sediments: An annual study. Marine Ecology Progress Series **200**:59-76.

Svensson, J. R., M. Lindegarth, and H. Pavia. 2010. Physical and biological disturbances interact differently with productivity: Effects on floral and faunal richness. Ecology **91**:3069-3080.

Sweeney, R. E., E. K. Kalil, and I. R. Kaplan. 1980. Characterization of domestic and industrial sewage in Southern-California coastal sediments using nitrogen, carbon, sulfur and uranium tracers. Marine Environmental Research **3**:225-243.

Swilling, W. R., M. C. Wooten, N. R. Holler, and W. J. Lynn. 1998. Population dynamics of Alabama beach mice (*Peromyscus polionotus ammobates*) following Hurricane Opal. American Midland Naturalist **140**:287-298.

Szczucinski, W., N. Chaimanee, P. Niedzielski, G. Rachlewicz, D. Saisuttichai, T. Tepsuwan, S. Lorenc, and J. Siepak. 2006. Environmental and geological impacts of the 26 December 2004 tsunami in coastal zone of Thailand - Overview of short and long-term effects. Polish Journal of Environmental Studies **15**:793-810.

Takahashi, K., T. Yoshioka, E. Wada, and M. Sakamoto. 1990. Temporal variations in carbon isotope ratio of phytoplankton in a eutrophic lake. Journal of Plankton Research **12**:799-808.

Takai, N., Y. Mishima, A. Yorozu, and A. Hoshika. 2002. Carbon sources for demersal fish in the western Seto Inland Sea, Japan, examined by delta C-13 and delta N-15 analyses. Limnology and Oceanography **47**:730-741.

Takami, H., N.-I. Won, and T. Kawamura. 2013. Impacts of the 2011 mega-earthquake and tsunami on abalone *Haliotis discus hannai* and sea urchin *Strongylocentrotus nudus* populations at Oshika Peninsula, Miyagi, Japan. Fisheries Oceanography **22**:113-120.

Tam, N. F. Y. and Y. S. Wong. 2000. Spatial variation of heavy metals in surface sediments of Hong Kong mangrove swamps. Environmental Pollution **110**:195-205.

Tanabe, S. and A. Subramanian. 2011. Great eastern Japan earthquake - possible marine environmental contamination by toxic pollutants. Marine Pollution Bulletin **62**:883-884.

Tarutani, K., Y. Niimura, and T. Uchida. 2004. Short-term uptake of dissolved organic nitrogen by an axenic strain of *Ulva pertusa* (Chlorophyceae) using N-15 isotope measurements. Botanica Marina **47**:248-250.

Taylor, D. I. 2003. 24 months after "offshore transfer": An update of water quality improvements in Boston Harbour.

Taylor, J. L. and C. H. Saloman. 1969. Some effects of hydraulic dredging and coastal development in Boca-Ciega-Bay, Florida. United States Fish and Wildlife Service Fishery Bulletin **67**:213-&.

Taylor, M. W. and T. A. V. Rees. 1999. Kinetics of ammonium assimilation in two seaweeds, *Enteromorpha* sp (Chlorophyceae) and *Osmundaria colensoi* (Rhodophyceae). Journal of Phycology **35**:740-746.

Tenore, K. R., L. F. Boyer, R. M. Cal, J. Corral, C. Garciafernandez, N. Gonzalez, E. Gonzalezgurriaran, R. B. Hanson, J. Iglesias, M. Krom, E. Lopezjamar, J. McClain, M. M. Pamatmat, A. Perez, D. C. Rhoads, G. Desantiago, J. Tietjen, J. Westrich, and H. L. Windom. 1982. Coastal upwelling in the Rias Bajas, NW Spain - contrasting the benthic regimes of the Rias de Arosa and de Muros. Journal of Marine Research **40**:701-772.

Tewfik, A., J. B. Rasmussen, and K. S. McCann. 2007. Simplification of seagrass food webs across a gradient of nutrient enrichment. Canadian Journal of Fisheries and Aquatic Sciences **64**:956-967.

Thistle, D. 1981. Natural physical disturbances and communities of marine soft bottoms. Marine Ecology Progress Series **6**:223-228.

Thompson, R. C., T. P. Crowe, and S. J. Hawkins. 2002. Rocky intertidal communities: Past environmental changes, present status and predictions for the next 25 years. Environmental Conservation **29**:168-191.

Thornber, C. S., P. DiMilla, S. W. Nixon, and R. A. McKinney. 2008. Natural and anthropogenic nitrogen uptake by bloom-forming macroalgae. Marine Pollution Bulletin **56**:261-269.

Thrush, S. F., J. E. Hewitt, M. Gibbs, C. Lundquist, and A. Norkko. 2006. Functional role of large organisms in intertidal communities: Community effects and ecosystem function. Ecosystems **9**:1029-1040.

Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature **441**:629-632.

Tucker, J., N. Sheats, A. E. Giblin, C. S. Hopkinson, and J. P. Montoya. 1999. Using stable isotopes to trace sewage-derived material through Boston Harbor and Massachusetts Bay. Marine Environmental Research **48**:353-375.

Turkington, R., E. Klein, and C. P. Chanway. 1993. Interactive effects of nutrients and disturbance - an experimental test of plant strategy theory. Ecology **74**:863-878.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. Ecosystems **1**:511-523.

Turner, S. J., J. E. Hewitt, M. R. Wilkinson, D. J. Morrisey, S. F. Thrush, V. J. Cummings, and G. Funnell. 1999. Seagrass patches and landscapes: The influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. Estuaries **22**:1016-1032.

Underwood, A. J. 1989. The analysis of stress in natural-populations. Biological Journal of the Linnean Society **37**:51-78.

Underwood, A. J. 1997. Experiments in ecology: Their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, UK.

Underwood, G. J. C. and J. Kromkamp. 1999. Primary production by phytoplankton and microphytobenthos in estuaries. Pages 93-153 *in* D. B. Nedwell and D. G. Raffaelli, editors. Advances in Ecological Research, Vol 29: Estuaries.

Underwood, G. J. C., J. Phillips, and K. Saunders. 1998. Distribution of estuarine benthic diatom species along salinity and nutrient gradients. European Journal of Phycology **33**:173-183.

Urbina, M., K. Paschke, P. Gebauer, and O. R. Chaparro. 2010. Physiological energetics of the estuarine crab *Hemigrapsus crenulatus* (Crustacea: Decapoda: Varunidae): responses to different salinity levels. Journal of the Marine Biological Association of the United Kingdom **90**:267-273.

URS. 2004. Assessment of environment effects: Christchurch City Council ocean outfall pipeline. Prepared for the Chirstchurch City Council

Valiela, I., J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. Limnology and Oceanography **42**:1105-1118.

Valiela, I., G. Tomasky, J. Hauxwell, M. L. Cole, J. Cebrian, and K. D. Kroeger. 2000. Operationalizing sustainability: Management and risk assessment of land-derived nitrogen loads to estuaries. Ecological Applications **10**:1006-1023.

Van Colen, C. 2009. Tidal flat macrobenthos ecology, recolonisation and succession. PhD. Ghent University

Van Dover, C. L., J. F. Grassle, B. Fry, R. H. Garritt, and V. R. Starczak. 1992. Stable isotope evidence for entry of sewage-derived organic material into a deep-sea food web. Nature **360**:153-156.

van Houte-Howes, K. S. S., S. J. Turner, and C. A. Pilditch. 2004. Spatial differences in macroinvertebrate communities in intertidal seagrass habitats and unvegetated sediment in three New Zealand estuaries. Estuaries **27**:945-957.

van Katwijk, M. M., A. R. Bos, P. Kennis, and R. de Vries. 2010. Vulnerability to eutrophication of a semi-annual life history: A lesson learnt from an extinct eelgrass (*Zostera marina*) population. Biological Conservation **143**:248-254.

Vanselow, K. A., M. Kolb, and T. Fickert. 2007. Destruction and regeneration of terrestrial, littoral and marine ecosystems on the Island of Guanaja/Honduras seven years after Hurricane Mitch. Erdkunde **61**:358-371.

Viana, I. G., J. A. Fernandez, J. R. Aboal, and A. Carballeira. 2011. Measurement of delta N-15 in macroalgae stored in an environmental specimen bank for

regional scale monitoring of eutrophication in coastal areas. Ecological Indicators **11**:888-895.

Villares, R. and A. Carballeira. 2004. Nutrient limitation in macroalgae (*Ulva* and *Enteromorpha*) from the Rias Baixas (NW Spain). Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I **25**:225-243.

Villnas, A., J. Norkko, K. Lukkari, J. Hewitt, and A. Norkko. 2012. Consequences of increasing hypoxic disturbance on benthic communities and ecosystem functioning. Plos One **7**.

Vizzini, S. and A. Mazzola. 2002. Stable carbon and nitrogen ratios in the sand smelt from a Mediterranean coastal area: Feeding habits and effect of season and size. Journal of Fish Biology **60**:1498-1510.

Voss, M. 2011. Nitrogen processes in coastal and marine ecosystems. Pages 147-176 *in* M. A. Sutton, Howard, C.M., Erisman, J.W., Billen, G., Bleeker, A., Grennfelt, P., van Grinsven, H., Grizzetti, B., editor. The European NItrogen Assessment. Cambridge University Press, Cambridge.

Voss, M., B. Larsen, M. Leivuori, and H. Vallius. 2000. Stable isotope signals of eutrophication in Baltic Sea sediments. Journal of Marine Systems **25**:287-298.

Wada, E., Hattori, A. 1978. Nitrogen isotopic effects in the assimilation of inorganic nitrogenous compounds by marine diatoms. Journal of Geomicrobiology **1**:85-101.

Wada, E., Kabaya, Y., Tsuru, K., Ishiwatari, R. 1990. ^{13}C and ^{15}N abundance of sedimentary organic matter in estuarine areas of Tokyo Bay, Japan. Mass Spectroscopy **38**:307-318.

Wada, E., H. Mizutani, and M. Minagawa. 1991. The use of stable isotopes for food web analysis. Critical Reviews in Food Science and Nutrition **30**:361-371.

Wada, E., M. Terazaki, Y. Kabaya, and T. Nemoto. 1987. N-15 and C-13 abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. Deep-Sea Research Part a-Oceanographic Research Papers **34**:829-841.

Waide, R. B. 1991. The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto-Rico. Biotropica **23**:475-480.

Waldbusser, G. G., R. L. Marinelli, R. B. Whitlatch, and P. T. Visscher. 2004. The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. Limnology and Oceanography **49**:1482-1492.

Wang, J. Q., X. D. Zhang, L. F. Jiang, M. D. Bertness, C. M. Fang, J. K. Chen, T. Hara, and B. Li. 2010. Bioturbation of burrowing crabs promotes sediment turnover and carbon and nitrogen movements in an estuarine salt marsh. Ecosystems **13**:586-599.

Wang, X. Q., L. J. Thibodeaux, K. T. Valsaraj, and D. D. Reible. 1991. Efficiency of capping contaminated bed sediments *in situ* .1. Laboratory-scale experiments on diffusion adsorption in the capping layer. Environmental Science & Technology **25**:1578-1584.

Warwick, R. M. 1986. A new method for detecting pollution effects on marine macrobenthic communities. Marine Biology **92**:557-562.

Warwick, R. M. and K. R. Clarke. 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. Marine Ecology Progress Series **129**:301-305.

Waser, N. A. D., P. J. Harrison, B. Nielsen, S. E. Calvert, and D. H. Turpin. 1998. Nitrogen isotope fractionation during the uptake and assimilation of nitrate,

nitrite, ammonium, and urea by a marine diatom. Limnology and Oceanography **43**:215-224.

Watt, I., T. Woodhouse, and D. A. Jones. 1993. Intertidal cleanup activities and natural regeneration on the Gulf-coast of Saudi-Arabia from 1991 to 1992 after the 1991 Gulf oil-spill. Marine Pollution Bulletin **27**:325-331.

Wattayakorn, G. 2002. Assessment of potential nutrient release from dredging activities. Battelle Press, Columbus.

Webb, A. P. and B. D. Eyre. 2004. Effect of natural populations of burrowing thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and denitrification. Marine Ecology Progress Series **268**:205-220.

Webster, I. T. and G. P. Harris. 2004. Anthropogenic impacts on the ecosystems of coastal lagoons: Modelling fundamental biogeochemical processes and management implications. Marine and Freshwater Research **55**:67-78.

Wefer, G. and J. S. Killingley. 1986. Carbon isotopes in organic-matter from a benthic alga *Halimeda-incrassata* (Bermuda) - effects of light-intensity. Chemical Geology **59**:321-326.

Welch, E. B., Cooke, G.D. 1999. Effectiveness and longevity of phosphorus inactivation with alum. Lake and Reservoir Management **15**.

Wells, A., R. P. Duncan, and G. H. Stewart. 2001. Forest dynamics in Westland, New Zealand: the importance of large, infrequent earthquake-induced disturbance. Journal of Ecology **89**:1006-1018.

Welsh, B. L. 1980. Comparative nutrient dynamics of a marsh-mudflat ecosystem. Estuarine and Coastal Marine Science **10**:143-164.

Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. Journal of Geology **30**:377-392.

Whanpetch, N., M. Nakaoka, H. Mukai, T. Suzuki, S. Nojima, T. Kawai, and C. Aryuthaka. 2010. Temporal changes in benthic communities of seagrass beds impacted by a tsunami in the Andaman Sea, Thailand. Estuarine Coastal and Shelf Science **87**:246-252.

White, P. S., Pickett, S.T.A. . 1985. Natural disturbance and patch dynamics: An introduction. Page 472 *in* S. T. A. Pickett, White, P.S., editor. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, CA.

Whitlatch, R. B. 1977. Seasonal changes in the community structure of the macrobenthos inhabiting the intertidal sand and mud flats of Barnstable Harbour, Masswachusetts. Biological Bulletin **152**:275-294.

Whitlatch, R. B. 1980. Patterns of resource utilization and coexistence in marine inter-tidal deposit-feeding communities. Journal of Marine Research **38**:743-765.

Whitlatch, R. B., A. H. Hines, S. F. Thrush, J. E. Hewitt, and V. Cummings. 1997. Benthic faunal responses to variations in patch density and patch size of a suspension-feeding bivalve. Journal of Experimental Marine Biology and Ecology **216**:171-189.

Widdicombe, S. and M. C. Austen. 2001. The interaction between physical disturbance and organic enrichment: An important element in structuring benthic communities. Limnology and Oceanography **46**:1720-1733.

Wiencke, C. and G. Fischer. 1990. Growth and stable carbon isotope composition of cold-water macroalgae in relation to light and temperature. Marine Ecology Progress Series **65**:283-292.

Wilkinson, M., Telfer, T.C. Grundy, S. 1995. Geographical variations in the distribution of macroalgae in estuaries. Netherlands Journal of Aquatic Ecology **29**:359-368.

Will, T. 1991. Birds of a severely hurricane-damaged Atlantic Coast rain-forest in Nicaragua. Biotropica **23**:497-507.

Willig, M. R. and G. R. Camilo. 1991. The effect of Hurricane Hugo on 6 invertebrate species in the Luquillo Experimental Forest of Puerto-Rico. Biotropica **23**:455-461.

Wilson, R. S., S. Heislers, and G. C. B. Poore. 1998. Changes in benthic communities of Port Phillip Bay, Australia, between 1969 and 1995. Marine and Freshwater Research **49**:847-861.

Wong, W. W. and W. M. Sackett. 1978. Fractionation of stable carbon isotopes by marine-phytoplankton. Geochimica et Cosmochimica Acta **42**:1809-1815.

Woods, C. M. C. and D. R. Schiel. 1997. Use of seagrass *Zostera novazelandica* (Setchell, 1933) as habitat and food by the crab *Macrophthalmus hirtipes* (Heller, 1862) (Brachyura: Ocypodidae) on rocky intertidal platforms in southern New Zealand. Journal of Experimental Marine Biology and Ecology **214**:49-65.

Woolbright, L. L. 1991. The impact of Hurricane Hugo on forest frogs in Puerto-Rico. Biotropica **23**:462-467.

Woolbright, L. L. 1997. Local extinctions of anuran amphibians in the Luquillo Experimental Forest of northeastern Puerto Rico. Journal of Herpetology **31**:572-576.

Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature **417**:848-851.

Wulff, F., A. Stigebrandt, and L. Rahm. 1990. Nutrient dynamics of the Baltic Sea. Ambio **19**:126-133.

Wunderle, J. M., J. E. Mercado, B. Parresol, and E. Terranova. 2004. Spatial ecology of Puerto Rican boas (*Epicrates inornatus*) in a hurricane impacted forest. Biotropica **36**:555-571.

Yamamuro, M. 1999. Importance of epiphytic cyanobacteria food sources for heterotrophs in a tropical seagrass bed. Coral Reefs **18**:263-271.

Yuksek, A., E. Okus, I. N. Yilmaz, A. Aslan-Yilmaz, and S. Tas. 2006. Changes in biodiversity of the extremely polluted Golden Horn Estuary following the improvements in water quality. Marine Pollution Bulletin **52**:1209-1218.

Zajac, R. N. and R. B. Whitlatch. 1982a. Responses of estuarine infauna to disturbance .1. Spatial and temporal variation of initial recolonization. Marine Ecology Progress Series **10**:1-14.

Zajac, R. N. and R. B. Whitlatch. 1982b. Responses of estuarine infauna to disturbance .2. Spatial and temporal variation of succession. Marine Ecology Progress Series **10**:15-27.

Zajac, R. N. and R. B. Whitlatch. 2001. Response of macrobenthic communities to restoration efforts in a New England estuary. Estuaries **24**:167-183.

Zajac, R. N., R. B. Whitlatch, and S. F. Thrush. 1998. Recolonization and succession in soft-sediment infaunal communities: the spatial scale of controlling factors. Hydrobiologia **375-76**:227-240.

Zeldis, J., Skilton, J.E., South, P.M., Schiel, D.R. 2011. Effects of the Canterbury earthquakes on Avon-Heathcote Estuary/Ihutai ecology. NIWA Client Report

No: CHC2011-101 prepared for Enviornment Canterbury and Christchurch City Council.

Zeman, A. J. 1994. Subaqueous capping of very soft contaminated sediments. Canadian Geotechnical Journal **31**:570-577.

Zhang, S. Y., Q. H. Zhou, D. Xu, J. D. Lin, S. P. Cheng, and Z. B. Wu. 2010. Effects of sediment dredging on water quality and zooplankton community structure in a shallow of eutrophic lake. Journal of Environmental Sciences-China **22**:218-224.

Zieman, J. C., S. A. Macko, and A. L. Mills. 1984. Role of seagrasses and mangroves in estuarine food webs - temporal and spatial changes in stable isotope composition and amino-acid content during decomposition. Bulletin of Marine Science **35**:380-392.